SOME FUNDAMENTAL MORPHOLOGICAL OBJECTIONS TO THE MUTATION THEORY OF DE VRIES

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THE hypothesis of the saltatory origin of species has received a new impetus from the investigations of De Vries,[*] published in his "Mutationstheorie" and subse-

[1] To an address delivered in Brussels before the outbreak of the war and published in Science (Vol. 40, No. 1020, July 17th.), Professor de Vries appends a criticism of the writers preliminary article on mutation, likewise published in Science (Vol 39, No. 1005, April 3d.). The gist of his objection to the writer's position, that Œnothera and other members of the Onagraceæ are in a position of hybrid contamination, as evidenced by the frequent sterility or partial sterility of their pollen, is the contention that pollen sterility and gametic sterility in general is not sufficient evidence of hybrid contamination. To this statement two replies may be made. In the first place prominent geneticists for many years have recognized pollen sterility as important evidence of hybridization. Secondly investigations, which have now become very extensive, on the Angiosperms as a whole, show very interesting conditions in many natural families. While the monotypic species and those which are isolated geographically or phenologically (that is by a time of flowering later or earlier than that of the mass of species belonging to the genus) have invariably good pollen, those species, which overlap in their geographical range and in their times of flowering in many cases are characterized by abortion of the reproductive cells. In other words pollen infertility is only found where the possibility of crossing is present. This principle has been illustrated in the body of the present article by reference to the Rosaceæ. Taking a further illustration from the large family Ranunculaceæ, *Ranunculus acris* and *R. repens,* which overlap both in range and time of flowering have pollen, which is often largely imperfect, particularly in the first mentioned species. *R. rhomboideus* on the other hand, flowering in the very early spring has perfect pollen development.

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quent works. The chief foundation for his views, in regard to the instantaneous origin of species, is furnished by the conduct of *Œnothera lamarckiana* in cultures. It has been somewhat generally recognized that *O. lamarckiana,* and more recently, other species of the genus as well, constitute crucial evidence in regard to the validity of the mutation hypothesis on the botanical side. A great many investigations on the genetics and cytology of *O. lamarckiana* and other species, as well as crosses between species and "mutants" of *Œnothera,* have been carried on during the past decade by De Vries, and his followers and opponents. As a result a huge and highly technical literature has grown up. *Œnothera* is obviously regarded, on the botanical side at any rate, as the touchstone of the mutation hypothesis as formulated by De Vries. Obviously if this genus does not stand the test of critical investigation, the mutation hypothesis, so far as its validity depends upon De Vries's chosen illustration, is discredited.

Since *Œnothera* and by obvious implication the Onagraceæ, to which it belongs, have become authority for the mutation hypothesis, in its latest revival, they must like Cæsar's wife be beyond suspicion. Like Cæsar, *Œnothera* has become a name of authority and its family affairs accordingly, should be beyond suspicion, when subjected to the most searching investigation. It is apparently just in this direction that the weak spot of the mutation hypothesis lies. Too much attention has apparently been given to ringing the changes on the so-called mutants of *Œnothera* and not enough to the investigation of the general morphological situation in the Onagraceæ, to which this much-discussed genus belongs.

Unusual variability in plants is ordinarily regarded as *prima facie* evidence of hybridism and the suggestion has in fact frequently been made by professional geneticists (*e. g.,* Bateson, Davis, East, Gates and others) that *Œnothera lamarckiana* is a hybrid. It is perhaps of interest in this connection to recall that one of the commonest expedients adopted by the practical breeder, for breaking

up the continuity of the germ plasm, is hybridization. Apposite in this connection is the wholesale hybridizing practised by Burbank, for the purpose of bringing about the necessary genetic plasticity in his cultures and thus obtaining by resultant mutation or variation, new and desirable varieties of useful plants. The morphological peculiarities of hybrids have been clearly recognized for nearly a hundred years. They are for example clearly set down in Gaertner's rare and classic prize essay, entitled "Versuche und Beobacthungen ueber die Bastarderzeugung im Pflanzenreich" (Stuttgart, 1849). Curiously enough these important criteria have been largely ignored by the adherents of the mutation hypothesis of De Vries. A very important and generally observed difference between hybrids and genetically pure species, is the very easily detected one of pollen sterility, partial or complete. Of course when the hybridizing forms show a considerable degree of compatibility, this character may be inconspicuous or even absent. Further even in cases where it is originally present, it may be subsequently largely eliminated by selection. De Vries himself has noted that about one third of the pollen of *O. lamarckiana* is abortive. The English geneticist Bateson was struck with this peculiarity of the species, so much discussed in recent years, in relation to its variable offspring in cultures and promptly and first called attention to the obvious significance of this feature, suggesting that *O. lamarckiana* was a hybrid and that its remarkable conduct was the result of hybridization. This objection has in reality never been met. It is the purpose of the present article to show on grounds commonly accepted by geneticists and morphologists, that not only is genus *Œnothera* in general characterized by genetically impure or hybrid species, but that the condition of genetical impurity is extremely common in the Onagraceæ as a whole.

It will be convenient to begin with the examination of our common and very variable garden *Fuchsias*, which belong to the family Onagraceæ. The common *Fuchsia*,

sometimes known to gardeners as *Fuchsia speciosa,* is recognized as a hybrid derivative of *Fuchsia magellanica,* a native of southern South America.   Fig. 1 illustrates
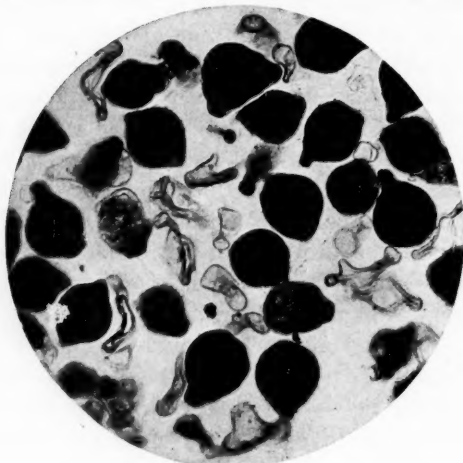

FIG. 1

photomicrographically, the condition of the pollen in one of the garden varieties of *Fuchsia.*   The sound pollen grains appear as dark bodies with two or more germination pores projecting from their surfaces.   The dark color of the grains is due to the deeply staining character of their protoplasmic contents.   More than a third of the pollen present in the anther cavity is abortive and is represented in the photograph by shrivelled light-colored objects, which are in fact empty and collapsed pollen grains.   In other varieties of the garden *Fuchsia,* the grains may either be entirely abortive and empty (as is the case for example in the so-called mutant of *Œnothera lamarckiana,* known as *O. lata*) or they may all be more or less well developed so far as their protoplasmic contents are concerned, but extremely varying in size.   In the present description, perfection or imperfection of pollen is judged only from the morphological aspect, because this is the significant point of view from the standpoint of the

detection of hybridization. Physiological sterility is frequently due to entirely different causes than genetical lack of harmony, as for example in the horseradish or the potato (*Solanum*). In the former it has been found possible to bring about the formation of fertile seed by simply girdling the top of the subterranean storage region of the plant, so as to prevent the undue descent of assimilates. The common white lily, *Lilium candidum,* presents a similar condition, for here the setting of seed takes place only when the leafy flowering axis is severed from its bulb and kept in water. So far as I am aware, there have been no experiments as to the result of severing the continuity of the phloem (girdling), in relation to the restoration of seed production in the potato. The common yellow day lily (*Hemerocallis*) possibly presents a case similar to that of *Lilium candidum,* for it does not ordinarily set seed, although in all the examples I have examined the pollen was morphologically perfect. I have not yet been able to secure flowers of any pure species of *Fuchsia,* a genus which flourishes mostly in the remoter parts of South America and in the New Zealand islands. The cultivation of *Fuchsias,* although once very popular, has now gone out of vogue and it is consequently difficult to secure specimens of the species. As has been pointed out the commonly cultivated *Fuchsias* are of hybrid origin.

We may now turn our attention to a very puzzling genus of the Onagraceæ, namely *Epilobium.* This genus has been a great riddle to systematists and the determination of species has been extremely difficult on account of their extreme variability. In European systematic works, this high degree of variability is recognized clearly to be largely due to hybridization and in such a standard work as the "Naturliche Pflanzenfamilien" of Engler and Prantl, the statement is definitely made that the various species of *Epilobium* frequently and commonly hybridize with one another in nature. Let us consider in this connection the northern hemisphere cosmopolitan species, known as *Epilobium angustifolium,* the willow herb or

fire weed, which by contrast to many of the other *Epilo-
biums,* is so constant and distinct that it is frequently
referred to a separate genus, *Chamænerion.* This species
shows its most marked distinction from other species of
Epilobium (*Epilobium* proper) in the fact that its pollen
grains are separate and not in tetrads, as is the case in
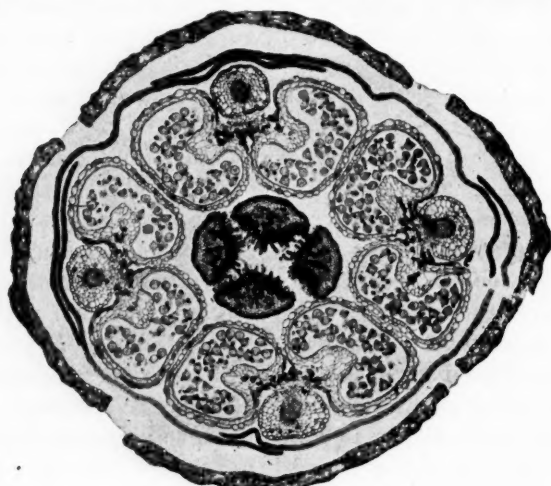other common species. Fig. 2 reproduces photograph-

Fig. 2

ically a transverse section of a mature flower bud of
E. (*Chamænerion*) *angustifolium.* On the outside are
seen the floral envelopes, two in number, composed, as is
the rule in the Onagraceæ, of four parts each. Within lie
four stamens represented by their anther sacks and inter-
nal to these are four stigmas representing the carpellary
or ovarial portion of the flower. The photograph is on a
sufficient scale of magnification to show the pollen grains
in the loculaments or cavities of the anthers. Obviously
the pollen is very uniform and perfect in its development.
Fig. 3, likewise photographic, illustrates the organization
of the pollen as viewed with a much higher magnification
of the microscope. Although some of the grains are only

partially included in the plane of section, it is quite clear, that like those of *Fuchsia*, figured above, they have projecting germination pores, but unlike the *Fuchsia* of our illustration, all the pollen grains of *Epilobium* (*Chamæ-nerion*) *angustifolium* are perfectly developed. I have examined the pollen of the species under discussion from widely separate geographical regions and under different conditions of growth and season, with the uniform result,
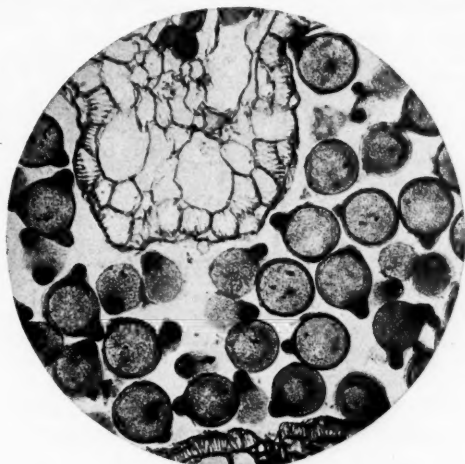

Fig. 3

that the pollen is perfect and invariable in any important respect. *E. angustifolium* is a species which apparently is not known to hybridize with other species and indeed it is not easy to see how it could cross with those having their pollen grains in tetrads. The perfection of the pollen in view of this condition appears particularly significant. The failure of *E. angustifolium* to hybridize in nature with other species of the genus is doubtless due to the fact that it is morphologically very distinct from these and would in all probability produce, if artificially crossed, only sterile hybrids.

We may now turn by way of comparison to a species of *Epilobium* of the ordinary type. Fig. 4 illustrates

photographically the floral organization of *Epilobium hirsutum,* as seen in transverse section of the bud just about to open. The illustration shows the floral envelopes
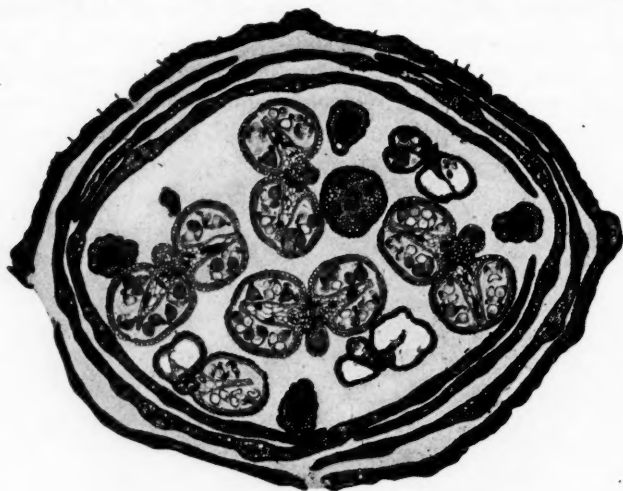

Fig. 4

and the stamens, together with the pistillary portion of the flower, the latter being somewhat displaced in the figure and cut through the region of the style. The long hairs characteristic of the calyx of this species have been trimmed off, for the purpose of facilitating photo-mechanical reproduction. As in the two illustrations above, the anther sacks are the most significant feature. Even with the low magnification employed for the purpose of illustrating the whole flower, the pollen grains in the loculaments of the anthers are easily discernible and present a striking contrast to those of *E. angustifolium,* in the respect that they are in groups of tetrads. Some of the groups are partially or wholly made up of individual grains without protoplasmic contents, which are smaller in size than the normal grains. Fig. 5 shows one of the anthers much more highly magnified. The anther walls, cavities and the pollen grains are now clearly distinguish-

able. Some of the grains are full size and present dark
contents. Others are considerably smaller and are devoid
of protoplasm. The latter are abortive or sterile grains.
We have in fact before us a hybrid derivative of *E. hir-
sutum,* commonly found near ballast in New England and
not unfrequently cultivated in gardens. Other species of
Epilobium in the stricter sense of the generic appellation,
show similarly abortive pollen development and the con-
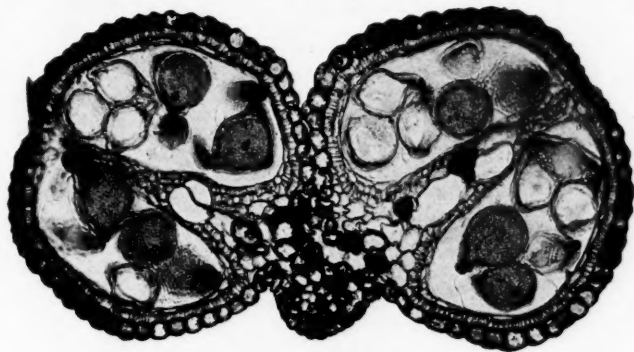clusion reached by old world systematists on the external

FIG. 5

characters, that hybridization is common among the spe-
cies of *Epilobium* proper, is entirely confirmed by the
study of the pollen. It need hardly be emphasized in this
connection, that imperfect pollen development has been
recognized for nearly a century by scientific plant breed-
ers, as a criterion of hybrids.

The genus *Œnothera* may now be profitably considered.
Fig. 6 presents a magnified view of a transverse section of
a mature flower bud of one of the commonest of eastern
species of *Œnothera,* namely *Œnothera biennis.* The
floral envelopes are more voluminous than in the two
genera illustrated above. Within are the stamens and in
the center of the figure the style appears as a large
rounded structure. Even with the low magnification em-
ployed, it is easy to discern that the contents of the anther
sacks present a very different appearance from those of

Epilobium angustifolium. Many of the grains of pollen
are light colored and devoid of the protoplasm which
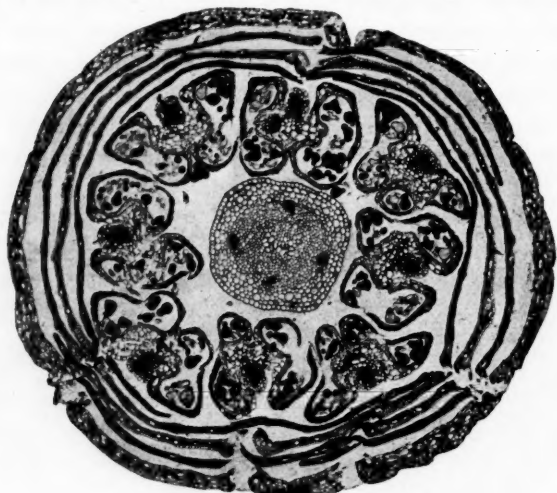gives a dark appearance to the sound grains. Fig. 7 illus-

Fig. 6

trates a single stamen under a high degree of magnifica-
tion. The characteristic layers of the wall of the anther
sack, described comparatively and in detail in the classic
memoir of Chatin, can readily be distinguished. Within
lie the pollen grains. Clearly only a few of these are fully
developed and possess normal protoplasmic contents.
The greater number are shrivelled and empty. Judged
from the generally accepted canon of the abnormalities of
hybrids, *O. biennis* is of hybrid origin. This view of its
nature is in harmony with its wide degree of inconstancy
throughout its very extended range. This feature is
doubtless responsible for the fact that the genus *Œnothera*
is at the present time undergoing considerable elaboration,
on the part of systematists. I have satisfied myself that
the pollen peculiarities of *O. biennis* are uniformly pres-
ent in specimens collected hundreds of miles apart, from
the Province of Ontario, the shores of the Gulf of St.

Lawrence and the New England States. I have further examined a large number of species of *Œnothera* from various parts of the continent and in every instance have found a greater or smaller amount of abortive pollen as a characteristic feature of the anther contents. De Vries in his "Mutationstheorie" describes the abortive condition of about one third of the grains in *O. lamarckiana.* This feature has been seized upon with insight by Bateson, as indicating the hybrid origin of *O. lamarckiana.* It is extremely curious that its significance should have

FIG. 7

escaped De Vries and his numerous disciples on this continent. Not only is *O. lamarckiana* itself characterized by a large proportion of abortive pollen but its so-called mutants are similarly characterized. In the feebler "elementary species" the pollen is often almost entirely abortive (*O. nanella*) and this is also generally the situation in *O. lata.* It should be further noted in this connection that if *O. lamarckiana* is of hybrid origin, the same statement must hold of the other species of *Œnothera*, since like this much-disputed one, they are similarly characterized, so far as they have been studied, by two correlated features, namely more or less abortive pollen and the peculiarity of throwing so-called mutants or "elementary species" in cultures. As a consequence of this condition,

it becomes more or less a superfluity to study any partic-
ular species of *Œnothera* from the genetical and morpho-
logical standpoint, since it is the genus as a whole which
manifests the peculiar features, which have brought it so
much into the foreground of biological controversy during
the past decade. This is on the whole a satisfactory situa-
tion as it enables us to cut the perplexing gordian knot
involving the controverted origin of *O. lamarckiana*.
The mutation hypothesis of De Vries accordingly turns
not upon the finding of new herbarium specimens which
may throw light upon the origin of a particular species
but upon the much larger question of the genetical status
of the genus *Œnothera* as a whole. This question can be
settled only by consideration of the Onagraceæ as a whole
and of other families of the Angiosperms, which present
similar reproductive peculiarities.

Before proceeding however to the discussion of the
facts recorded above in their relation to the mutation
hypothesis of De Vries, based on the conduct of *O. lamarck-
iana* in cultures, it will be necessary to make some brief
reference to other studies carried on in the laboratories of
plant morphology of Harvard University, which will be
published elsewhere, either at the present time or at a
later period. Obviously of great importance in the pres-
ent connection is a comparison of the conditions of spo-
rogeny found among the lower plants, the Bryophyta, the
Pteridophyta and Gymnosperms, which are not character-
ized by enormous multiplication of species, with the
sporogenic features of the Angiosperms in which the
multiplication of species has run riot. Further compari-
son of liverworts, belonging to the Marchantiales, Antho-
sperms, manifesting similar sporogenic and specific pecu-
liarities, is both pertinent and necessary, in the present
connection.

It will be convenient to deal first summarily with the
sporogenic conditions found in the lower forms of the
Embryophyta from the Bryophyta to the Gymnosperms.
In the present connection a considerable number of spe-

cies of liverworts, belonging to the Marchantiales, Antho-
cerotales and Jungermanniales, both acrogynous and
anacrogynous have been examined with the general result
that the only sterile cells present in the capsule cavities
were the elaters. Infertile spores and hybridism both were
conspicuous by their absence in the forms studied. The
same statement *mutatis mutandis* holds for the true
mosses. Some indication of spore abortion was detected
in the extremely variable genus *Sphagnum*. It would
seem that natural hybrids exist to some extent in this
genus. Among the Pteridophyta both the Lycopsida and
Pteropsida were studied. None of the numerous Lycopsid
forms investigated showed signs of spore abortion or
hybridism. Among the Pteropsida, the only well-known
hybrids are found among what is probably the highest
family, the Polypodiaceæ. There is a considerable litera-
ture upon hybrid ferns, in which references to spore abor-
tion as an accompanying feature are common. No evi-
dence of hybridism in the form of abortive spores was
found in examples of the Marattiaceæ, Ophioglossaceæ,
Osmundaceæ, Gleicheniaceæ, etc., were found, although a
large amount of material was examined. Among the
Gymnosperms, the Cycadales, Ginkgoales, Coniferales
and Gnetales were examined. The Coniferales yielded
only a single species of *Abies,* which showed evidence by
the presence of abortive pollen grains of hybrid origin.
The genus *Pinus* is very old and its species accordingly
very distinct. Not the slightest evidence of hybridization
was found here or in other numerous and widely distrib-
uted species of conifers, other than *Abies* mentioned
above. This does not of course preclude the discovery of
such conditions later. The writer has had the opportunity
of examining the spores of a number of fossil forms from
the Paleozoic and Mesozoic, still contained within the
sporangia, and in no case were abortive spores recognized.
The general conclusion can be drawn from the forms just
considered that hybridism is rare among them and that

where it occurs it is accompanied by the phenomenon of spore abortion.

If we turn to the Angiosperms with their nearly one hundred and fifty thousand recognized species, we find that hybridism is very commonly recognized. It would take us much too far to discuss the situation here at any length. The consideration of a single important family must suffice. The one chosen, as being of particular significance in the present connection, is the Rosaceæ. We have had a recognition for many years past on the part of systematic botanists in this country and in Europe that hybridism is extremely common as a natural condition in certain genera of the Rosaceæ. The inference in such cases is generally based on the blended character of the hybrids themselves, which show to a large extent a combination of the characters of their parent species. Professor Brainerd has recently made some very interesting investigations in this direction in the case of American representatives of the Rosaceæ. The recognized hybrid forms in the Rosaceæ are usually characterized by a considerable degree of pollen sterility, unless the parents happen to be species not very remote in relationship. In addition to the recognized hybrids of the rosaceous species, the work carried on in the Harvard laboratories has revealed a large number of hidden hybrids or crypthybrids, which are quite constant in their characters and are recognized by systematists as good species, but differ from normal species in the fact that their reproductive cells are to a greater or less degree abortive. Species of this kind are extremely common among those rosaceous genera, which have become of economic importance, such as *Rubus, Rosa, Pyrus, Malus, Sorbus, Cratægus,* etc. Taking *Rosa* as an illustration, in addition to numerous recognized hybrids, there are many types recognized as good species, *e. g., Rosa blanda,* in which the pollen is normally largely abortive, in still other species, frequently those which are isolated geographically, the pollen is quite sound, *e. g., Rosa rugosa* of Japan. The latter type of species must be

regarded as a species in the strict sense, while those of
the type of *Rosa blanda,* in which abortive pollen similar
to that characteristic of forms clearly recognized as hy-
brids, is present, are hidden hybrids. It follows that in
Rosa (or practically any of the other rosaceous genera
cited above), there are three types of individuals, namely
good species, hidden hybrids and open hybrids. The
middle condition is extremely common among the Angio-
sperms and is of the greatest importance in connection
with clear views in regard to the origin of species. Obvi-
ously constant or relatively constant hybrids can not rank
with pure species, such as are characteristic for example
of the Gymnosperms, in discussions in regard to the
origin of species by mutation or otherwise. The conduct
of such forms is conditioned to a greater or less extent by
their mixed blood. We may appropriately designate obvi-
ous hybrids as phenhybrids and those hybrids which are
recognizable as such by their internal morphological char-
acters as crypthybrids. Crypthybrids will probably when
studied more extensively in cultures by the geneticist, give
evidence of their hybrid origin in cultures. There can
be no doubt that many of the recognized species of the
Angiosperms are in reality crypthybrids. The enormous
multiplication of species in this great group of plants is
in all probability largely related to hybrid crossing. It
is of the utmost importance however to keep clearly in
mind that such hybrid species or crypthybrids are not at
all in the position of true species from the evolutionary
standpoint and that conclusions derived from their study
can not be applied without large reserves, to the question
of the origin of species in the strict sense. The species of
Pinus, so far as we have any evidence, since the main
types are known to have existed well back into the Meso-
zoic, in all probability illustrate the origin of species some-
what along the lines of the Darwinian hypothesis. On the
other hand the species of *Rosa* present obviously an
entirely different problem in evolution and the necessity
of making distinctions if we are to reach any definite bio-

logical goal is very clear. A great deal of the pessimism which at the present time is sending too many biologists after strange gods in other scientific shrines is doubtless to be traced to the failure to make this distinction. It may not be possible to make the distinction in all cases even among the higher plants; but it certainly will be necessary to realize its significance. Probably plants will in regard to this possibility enjoy in this respect, as in so many others, an advantage over animals in the studies of the experimental evolutionist.

We may now consider with advantage the status of the species of the genus *Œnothera*. The pollen sterility which characterized them all to a greater or less degree is indisputable evidence of their probable hybrid origin. The general situation in regard to the criteria of hybridism in plants has been recognized for nearly a hundred years. It has been made clear by Bateson in regard to *Œnothera lamarckiana*. The observations chronicled here appear to make it obvious that all the species of *Œnothera* are in the same boat genetically, that is that they are all of hybrid origin. They likewise probably will all be found to "mutate" just as *O. lamarckiana, O. biennis,* etc., are already known to do. It may appear later that there are certain species which have escaped, through geographical isolation or other causes, the mingling of blood, which is certainly characteristic of the *Œnotheras* of the Eastern United States. So far as we know them at present, the species of *Œnothera* are obviously in the same position as such species as *Rosa blanda,* that is they are crypthybrids. Doubtless the peculiarities of *O. lamarckiana, O. biennis,* etc., can be more clearly explained in the present condition of our knowledge as the result of hybrid origin than in any other way. It follows that the doctrine of mutation so far as it depends for its support upon the *Œnotheras* is in a discredited condition, as an explanation, in any proper sense of the term, of the origin of species.

Conclusions

1. The Onagraceæ are largely characterized by hybrid contamination in nature.

2. This statement holds with particular force for *Œnothera lamarckiana* and other species of the genus *Œnothera,* which have served as the most important basis of the mutation hypothesis of De Vries.

3. Constant hybrids or crypthybrids are of very common occurrence among the Angiosperms and have been illustrated in the present article by reference to the genetical conditions occurring in certain Rosaceæ.

4. The species of *Œnothera* are to a large extent, if not wholly, crypthybrids.

5. The objection raised by Bateson to the genetical purity of *Œnothera lamarckiana* is confirmed and is extended to the Onagraceæ in a general way, as well as to other species of *Œnothera.*

6. Hybridism is the best explanation yet put forward of the peculiar conduct of *Œnothera lamarckiana,* as well as other species of the genus in cultures.

7. The mutation hypothesis of De Vries, so far as it is supported by the case of *Œnothera lamarckiana,* is invalidated.
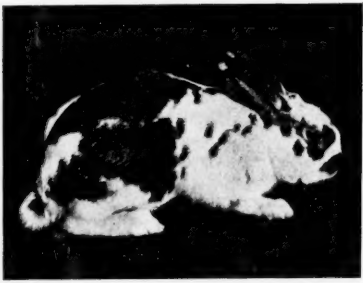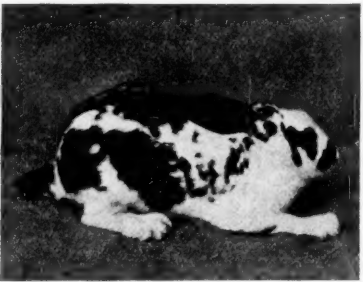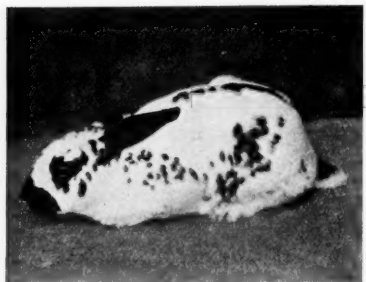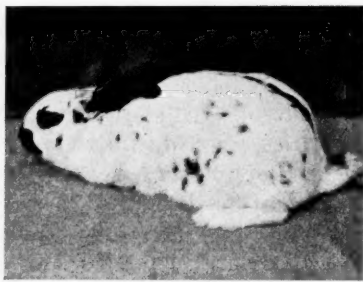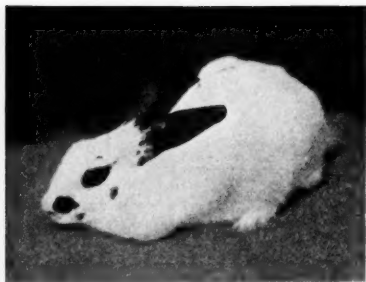
FIGS. 1 AND 2 AT TOP; FIGS. 3 AND 4 IN THE MIDDLE; FIGS. 5 AND 6 AT BOTTOM. Figs. 1–4, Photographs of Four English Rabbits forming a Graded Series in Amount of Colored Fur. These were adopted as our standard Grades 1–4, in terms of which all the rabbits described in these experiments have been classified. Fig. 5, Rabbit ♂21A, Father of the Series I Young. Fig. 6, Rabbit ♂40A, Father of the Series II Young.

THE ENGLISH RABBIT AND THE QUESTION OF MENDELIAN UNIT–CHARACTER CONSTANCY

W. E. CASTLE AND PHILIP B. HADLEY [1]

WHATEVER the theoretical importance of Mendel's law, its practical utility depends largely upon the purity of the gametes. If Mendelian unit-characters can through hybridization be recombined in desirable ways *without essential modification* during the process, Mendel's law is evidently a distinct acquisition to the practical breeder. Nevertheless, if crossing is likely to produce considerable changes in the characters which it is desired to combine in a new race, it is evident that Mendelian crosses must be used judiciously and with caution by the practical breeder.

Considerations such as these have led the senior author for several years to concentrate his studies of genetic problems upon the question of gametic purity. As a crucial experiment he conceived the plan of deriving an entire race of animals, not from a single *pair* of ancestors, but from a single *gamete,* so far as concerns a particular unit-character. It was thought that in a race so derived, if the principle of gametic purity holds, there should be no variation whatever in the particular unit-character concerned.

Color patterns of mammals seemed especially well adapted for such studies, since they are early differentiated and clearly Mendelize in crosses. The so-called "English" piebald rabbit presents an especially fine example of such a color pattern. The figures give a good idea of this striking pattern in which white and colored areas are interspersed much as in the "coach-

dog.'' It would be a distinct gain to breeders if they could reduce the variation in details of the English pattern so that ''prize-winners'' could be bred without the production of so many ''wasters,'' which depart in essential points from the standard pattern adopted for the breed. This was an additional reason for undertaking work with the English rabbit.

The first standard-bred English rabbits which the senior author had under observation, when mated *inter se,* produced young of three sorts. About half the young were fairly good ''standard'' English extensively marked with colored spots (see Fig. 3). About one fourth were much whiter than the standard demands, their spots being fewer and smaller (see Fig. 1). And the remaining fourth were without spots, that is, were self colored. This last class was found to be recessive and not to produce English offspring, if mated *inter se.*

The *whiter-than-standard* English proved to be homozygous for the pattern, the ''standard'' English being heterozygous and breeding like their parents.

From these observations it was clear (1) that the English pattern is a Mendelian dominant and (2) that the breeding of English rabbits resembles that of blue Andalusian fowls. For the standard-bred animal is a heterozygote in the production of which there is bound to be a constant production of ''wasters'' unless either the standard is changed or the homozygote can be changed to conform with the standard, producing an animal with more color. In the latter case homozygotes could be bred with each other and wasters eliminated. The question whether the pattern can be changed becomes therefore one of practical as well as theoretical interest.

In making crosses of English with other breeds of rabbits, there was found to be considerable variation among the heterozygous English produced, some being much whiter than others, *i. e.,* having less extensive colored spots. Plus (dark) and minus (light) selections were made to see to what extent the pattern was capable

of modification. These selection experiments are still in progress, but will be reported upon at another time.

The single-gamete experiment, with which this report will deal, was placed in the hands of the junior author, who has carried it out at the Rhode Island Agricultural Experiment Station.

As foundation stock for the experiment a single *heterozygous* English rabbit of standard character (grade 2, Fig. 5) was selected. To mate with him, it was desired to obtain a distinct breed of rabbits, free from the English pattern, and as pure (uniform) in all respects as possible. For this purpose the "Belgian hare" was chosen. A buck and two does obtained from Mr. G. W. Felton, Cliftondale, Mass., were found to breed very true. From them was bred a stock of does very uniform in character, twelve of which, together with one of the parents (2*A*), were mated with the selected English buck which we may henceforth call by his record number ♂21*A*. The young thus produced will be called "Series I" offspring. About half of them were self (non-English), the remainder (187 in number) were English.[2] The latter, although all undoubtedly heterozygous, varied in whiteness from grade 1 to grade 4 (Figs. 1–4), the *modal* or commonest condition being about the same as that of the father (grade 2). The distribution of the young in relation to our grades is shown in Table I. Statistical treatment of the table gives the *average grade* of the young as 2.43, that is somewhat darker than the father. Inspection of the table shows that more than half of the young are *darker* than the father, which supports in a general way the statistical average grade. If we consider separately the average grade of the young produced by each

[2] The total number of young obtained from ♂21*A*, when mated with Belgian hare does, has been to the time of writing 436. The English young now number 210, the non-English (self) number 226. For Series II matings presently to be described the corresponding numbers of young are: English, 219, non-English 196, total 415. For Series I and II combined the numbers are: English 429, non-English 422, total 851. This is unmistakably a 1: 1 Mendelian ratio.

mother, we find that it ranges from 2.15 in the case of ♀18F, which had 5 English young, to 2.79 in the case of ♀16D, which had 14 English young. The average number of English young to a mother is 14.4.

After this series of matings had been completed, a second series was begun in which the same 13 females were mated with one of the darkest bucks produced in the Series I matings (a son of ♀16E). The selected buck was ♂40A (Fig. 6), grade 3.75, considerably darker than his father (Fig. 5). This series of matings produced 189 English young, together with a like number of self (non-English) young. The grade distribution of the English young is shown in Table I, Series II. All of the 13 mothers except one (♀16F) produced darker offspring in the Series II than in the Series I matings. The lowest average grade was shown by the young of ♀17G, viz., 2.44. For Series I matings the lowest average was 2.15. The highest average grade in the Series II matings was given by the young of ♀16E, viz., 3.50. For Series I matings the highest average was 2.78. Consequently, both maximum and minimum averages were higher in the Series II than in the Series I matings. The grand average of all the 189 Series II offspring was 2.92 as compared with 2.43, the average grade of the Series I young. Their modal grade is 3.25. The modal grade for Series I was 2.00. Since the mothers were identical in both series, the difference in the young can be attributed only to the difference in the fathers. The male used in the Series II matings differed genetically as well as somatically from his father, who sired the Series I young. Not only was he darker, but he also produced darker English young. Yet the father contained only a single dose (one gamete) of English pattern and the son derived his English pattern exclusively from this same source. Hence the English unit-character had changed quantitatively in transmission from father to son. This seems to us conclusive evidence against the idea of unit-character constancy, or "gametic purity." If unit-characters are not constant, selection

reacquires much of the importance which it was regarded as possessing in Darwin's scheme of evolution, an importance which many have recently denied to it.

TABLE I

SHOWING THE DISTRIBUTION OF GRADES OF OFFSPRING IN THE FIRST AND SECOND SERIES OF MATINGS FOR EACH INDIVIDUAL MOTHER

Mother	Series	Grades of Young													Totals		Average
		1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25	3.50	3.75	4.00	Ser. I	Ser. II	
16A	I					1	2	2							5		2.30
	II					3	1	1	2	1	7	3	3			21	3.03
16B	I		1		1	3	1	1	1	2			1		11		2.39
	II			1	1	2	1		1	2	1	3				12	2.67
16D	I					2	5			1	2	3	1		14		2.79
	II								3	1	6		2			12	3.19
16E	I			2		5		2	1	1			1		12		2.29
	II										1	3	1			5	3.50
16F	I	1				2	1	5	3	2		3			17		2.62
	II				1	2	1	3	3			1				11	2.48
16G	I		1	2		2	3	1	2	3	1				15		2.35
	II						1	2	2	3	1	2	1	1		13	3.06
16H	I			1		3	3	1	2	2	2	1	2	1	18		2.76
	II					3		2	1	1	8	2	2	1		20	3.06
17E	I		1	1	3	4	3	3	1	1	2	2			21		2.36
	II					1	2	5	5	3	4	4	2	1		27	2.97
17G	I			1	9	6	3	3	2	1	2	1	1		29		2.27
	II		1	1		1	1	1	1	1	1	1				9	2.44
18D	I		1			3	3	3		1	2	2			15		2.53
	II					2	1	2	3	1	2	5				16	2.91
18F	I				3	1						1			5		2.15
	II			1	1	2		4	2	1	1	2	2			16	2.97
18H	I			1	1		3	1	1	3					10		2.43
	II				1		3	3	4	2	3		1	2		19	2.87
2A	I		1	2	1	1	4	2	3	1					15		2.22
	II				1	2				1	2	2				8	2.78
Totals	I	1	5	10	18	33	31	24	16	18	11	13	6	1	187		2.43
	II		1	2	5	17	13	19	29	18	37	27	14	7		189	2.92

The question whether an imaginary "unit-factor" for English pattern has or has not changed in correlation with the visibly changed English unit-character is not here discussed. We recognize that it has an academic interest, which, however, scarcely affects the practical question whether the visible Mendelizing characters of animals are subject to change through crossing or through selection or both.

ON THE NUMBER OF RAYS IN ASTERIAS TENUISPINA LAMK. AT BERMUDA[1]

BY W. J. CROZIER

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I. It was suggested by Clark (1901) that the average number of rays borne by *Asterias tenuispina* was different for separate localities in Bermuda. He examined forty specimens of this species—eleven from Coney Island and twenty-nine from Harrington Sound; in the first set the average number of rays was 5.91 (I find the mode to be 6), in the second set 6.93 (with a mode of 7). If this condition really obtains, it would be an exceedingly interesting matter to determine the factors responsible for this sort of difference. I have therefore examined a number of *Asterias* (312 in all) from several localities in the Bermudas, namely: Agar's Island, Spanish Point, Hawkins Island, Ely's Harbor, Hungry Bay, Harrington Sound and Coney Island; the first four are situated on the periphery of Great Sound, the others at widely removed points on the north and south shores. For the identification of these places, references may be made to the maps published by Mark (1905).

These observations were made at the Bermuda Biological Station, mostly during the summer of 1914.

II. The first lot of starfishes was collected in the immediate vicinity of Agar's Island in 1913. The number of rays varied from 2 to 9; the frequency distribution is given in Fig. 1. The modal number of rays is clearly 7. In 1914 a collection of *Asterias* from this place gave the ray frequency distribution shown in Fig. 2, where the modal number of rays is again 7. Collections, during 1914, at the other stations named gave the following ray frequency counts:

[1] Contributions from the Bermuda Biological Station for Research, No. 35.

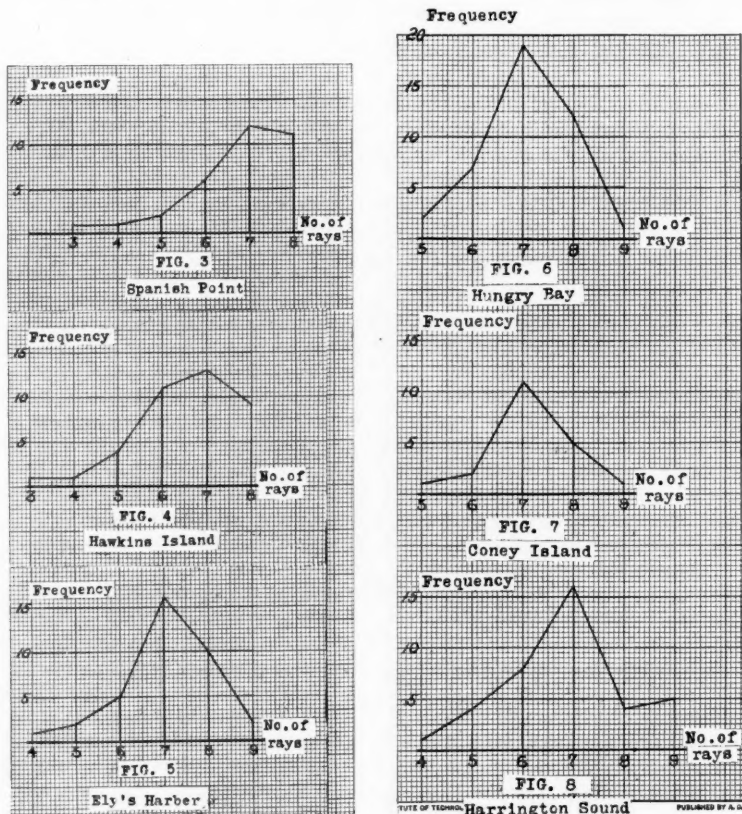| Station and Year	No. of Specimens	Modal Ray Number	See Figure
Agar's Isl., 1913	43	7	1
Agar's Isl., 1914	62	7	2
Spanish Point, 1914	33	7	3
Hawkins Isl., 1914	39	7	4
Ely's Harbor, 1914	36	7	5
Hungry Bay, 1914	41	7	6
Coney Island. 1914	20	7	7
Harrington Sound, 1914	38	7	8

The modal number of rays is in each case 7. This is true for the same locality in two successive years, for near-by localities and for places widely enough separated

FIG. I
Agar's Island - 1913

FIG. 2
Agar's Island - 1914.
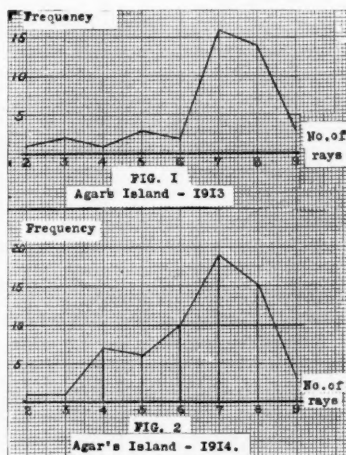
to yield critical data relative to the suggestion which prompted this inquiry. For the total population examined the ray frequency distribution, which of course gives a mode of 7 rays, is plotted in Fig. 3. It is to be noted further that according to Ludwig (1897, p. 345) the most common number of rays in *A. tenuispina* from the Mediterranean is also 7.

III. It has been observed by every one who has studied *A. tenuispina* that in most of the individuals the rays occur in two groups, those of one group being longer than those in the other, though within each group the rays are of about the same length. This condition is evident in 259 (83.6 per cent.) of my specimens. There is general

agreement (cf. Ludwig, 1897, and Ritter and Crocker, 1900), that in some cases, if not in all, "this disparity in size is due to the regeneration of halves of automatically bisected animals." My observations fully confirm this. I have witnessed, as did Ludwig, several cases of spon-

FIG. 3
Spanish Point

FIG. 4
Hawkins Island

FIG. 5
Ely's Harber

FIG. 6
Hungry Bay

FIG. 7
Coney Island

FIG. 8
Harrington Sound

taneous self-division in the laboratory. The casting off of one or more rays may at any time be induced by holding or injuring one or several rays, or by the stimulation of a ray with dilute acid applied with a pipette. The autotomy of a single ray takes place very much as described by King (1898) for *Asterias vulgaris;* the existence of a "breaking joint" in the region of the fifth ambulacral

ossicle is shown by the fact that even in preserved material the rays part very easily in that region.

The relative abundance of cases in which there are evident two groups of rays of different length indicates that, as in *Linckia* (Clark, 1913), autotomous division is a normal method of asexual reproduction.

FIG. 10

Distribution of ray frequencies among individuals with all rays of equal or nearly equal length

FIG. 9

Distribution of ray frequencies in the total population.

FIG. 11

Relation of long to short rays

IV. The numerical relations of the old rays to the regenerating ones, and the topographical arrangement of the latter, yield evidence relative to certain questions in the physiology of regeneration.

(*a*) It is to be observed that the regeneration in question has taken place apart from experimental control; therefore information as to the number of rays usually present just before *Asterias* undergoes self-division must be deduced from the data at hand. The modal-ray frequency for specimens with rays of very nearly equal length is 7 (Fig. 10), but it is a question whether this appearance of equality in ray length may not be due to a

variety of conditions, especially the rapid growth of re-
generated rays. The regenerating rays of *Linckia* (Clark,
1913; Monks, 1904) and the newly formed rays of multi-
radiate types (Ritter and Crocker, 1900) grow more rap-
idly than the old ones and soon reach the dimensions of
the latter; this is also indicated in my series. But the cor-
relation of the number of long with the number of short
rays (using only those cases in which the two groups were
clearly distinct) makes it evident (Fig. 11) that the condi-
tion in which there are 3 or 4 long rays and 4 short ones is
by far the most common; and further, that the cases in
which there are either 3 or 4 long rays are almost equally
abundant. It seems not unlikely, then, that *A. tenuispina*
usually has 7 rays before it divides, and that it divides
into two parts having, respectively, 3 and 4 rays, the divi-
sion-surface then giving rise, in the greater number of
cases, to 4 new rays, but sometimes to 5, 3 or even 2.

If all the individuals observed had undergone autotomy
and regeneration according to this scheme, then those
with 7 and those with 8 rays would be expected to occur
in equal abundance; 8 is next in frequency to 7, but the
latter preponderates because some starfishes have prob-
ably not autotomized at all, and because all the animals
which have divided do not adhere to this paradigm (see
Fig. 11). Yet, in the majority of cases, 4 rays are regen-
erated whether there are 2, 3 or 4 long (old) rays in
evidence.

It would seem that self-division may occur at any time
in the life history of *A. tenuispina,* or at least in animals
of all sizes, though it is my impression, gained from hand-
ling many live individuals, that the smaller (younger ?)
ones autotomize more readily than larger ones. Those
showing two distinct ray groups ranged in longer ray
length from 11 mm. to 65 mm. There is no evidence that
autotomous divisions follow one another rapidly, or in-
deed that they occur more than once in any given indi-
vidual.

One case was observed in which there was one long ray
only, and 6 shorter ones. This may mean that a single
ray can regenerate the whole body, as suggested by v.

Martens (1866, quoted by King, 1898) for this species. I have not been able to substantiate this idea by laboratory experiments, for, in my tests, single isolated rays did not live more than a few weeks.

(*b*) Newly forming rays have a tendency to appear in symmetrically disposed pairs (see Fig. 12), which gives to
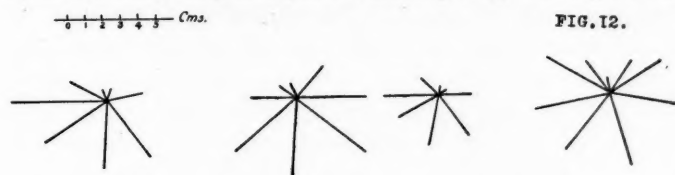
FIG. 12.

DIAGRAMATIC REPRESENTATION OF THE RAYS OF FOUR ASTERIAS, SHOWING TENDENCY OF RAYS TO APPEAR IN PAIRS. Measured from the mouth along the ventral side.
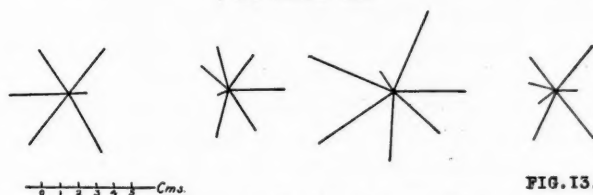
FIG. 13.

ILLUSTRATING THE RELATIONS OF NEW RAYS.

many individuals a strikingly bilateral aspect. This is accentuated by their behavior, for, in the absence of directive stimuli, they commonly move with the longest rays in advance. In moving away from the light, the locomotor movement of the group of longer rays also tends, in many cases, to produce a spurious "orientation." When placed oral side up, the larger rays exert a determining influence on the direction and manner of righting. These effects are due to the greater pedicel and muscle development of the longer, thicker, rays.

The formation of two rays at a radial cut on the disc was found by King (1900) in *Asterias vulgaris*.

V. I have suggested, above, that *Asterias* with 7 subequal rays have probably arrived at that condition by different routes. One method of ray multiplication appears to be the spontaneous addition of new rays at any point on the disc. Twelve starfish were found which showed but one ray markedly shorter than the others.

Of these, 4 had 5 long rays, 4 had 6, 2 had 7, 1 had 3 and 1 had 4 (see Fig. 11). The addition of new rays during adult life is, so far as known, unusual among starfish, excepting in the multiradiate forms (cf. Ritter and Crocker, 1900; Clark, 1907; M'Intosh, 1907). The twelve cases found in *A. tenuispina* may mean merely that a single ray has been cast off and is being regenerated, for there is found about the same percentage of naturally occurring regenerating examples of *A. vulgaris* (King, 1898; 1900). Yet I am inclined to interpret this condition as indicating the way in which the modal hepta-radiate form is derived from the fundamental penta-radiate one, or from a hexa-radiate plan, if the young of *A. tenuispina* be like the post-larvæ of *Pycnopodia* (Ritter and Crocker, 1900) previous to self-division.[3] The three smallest *Asterias* seen had 6 rays. These were subequal and $8 \pm$ mm. long. Other specimens, slightly larger, had either 7 or 8 rays.

Cases such as those illustrated in Fig. 13 may further prove that addition of new rays occurs independently of the reformation of rays subsequent to self-division.

VI. The number of madreporites in *A. tenuispina* is also variable, as noted by Ludwig (1897, p. 358) and others. The number of madreporic bodies is certainly not correlated with the size of the starfish. One of the smallest ones seen had 8 rays and 5 madreporites, its mean ray length being 10 mm.; while the largest animal collected had 5 rays, with a mean ray length of 70 mm., and but one madreporite. The table in Fig. 14, which includes all cases in which the madreporites were counted, shows that, while the distribution of these bodies is irregular, their number is to some extent correlated with the number of rays. Ludwig gave it as his opinion that there was no correlation of this sort. The relation stands out more clearly if only those individuals having equal rays (and therefore presumably "full grown") are included (Fig. 15). Unfortunately, the number of animals is small.

Multiple madreporites were noted in 5 out of 101 ex-

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[3] According to Clark's (1907) studies, the young *Heliaster* has five rays only; his results throw considerable doubt upon the correctness of the conclusions of Ritter and Crocker.

amples. Three of these showed a condition which might have arisen either by the fusion of two plates or by the

NUMBER OF RAYS

NUMBER OF MADREPORITES	2	3	4	5	6	7	8	9	
1	1	1	2	3	5	6	4		22
2		1	1	3	7	10	4	1	27
3					4	10	14		28
4					2	8	10	2	22
5						1	1		2
	2	3	6	19	34	33	3		101

FIG. 14
Correlation between number of madreporites and number of rays

NUMBER OF RAYS

NUMBER OF MADREPORITES	4	5	6	7	8	9	
1		2	1	1			4
2	1	2	1	2			6
3			1	4	2		7
4			1		2	1	4
		4	4	7	4	1	21

FIG. 15
Relation of ray frequency to number of madreporites in animals with rays of equal length

division of a single one. The other two cases were similar, but of trefoil form. Dissection showed, in each instance, that a single stone canal was present. Therefore these multiple plates had probably arisen by the division of an originally single one. (For a similar condition in *A. vulgaris,* see Davenport [1901].) Only one multiple madreporite was found in any one individual.

SUMMARY

1. The modal number of rays in *Asterias tenuispina* is 7. The range in ray number is from 2 to 9.

2. The 7-ray condition is uniformly the most frequent, even in widely separated localities.

3. The modal ray number is the same for animals with subequal rays as for those with a group of regenerating rays.

4. The evidence indicates that, *most commonly, A.*

tenuispina has 7 rays before it undergoes autotomy, that it divides into 3-ray and 4-ray portions, and that each of these parts regenerates 4 rays.

5. Regenerating rays tend to appear in bilaterally disposed pairs, as regards size.

6. There is no evidence that self-division occurs often in the life of individuals, though possibly it does.

7. New rays may be added at any point on the disc.

8. The number of madreporites varies from 1 to 5, and is to some extent correlated with the number of rays; it is not correlated with the size of the animal.

9. Double or triple madreporites occur in about 5 per cent. of the individuals.

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[1] "Phataria" is an error, as pointed out by Clark (1913).

SHORTER ARTICLES AND DISCUSSION

MR. MULLER ON THE CONSTANCY OF MENDELIAN FACTORS

In discussing the selection experiments of Phillips and myself with hooded rats,[1] Mr. Muller[2] accepts the explanation of " modifying factors " which we offered to account for certain peculiar results obtained, but rejects the idea which we also suggested, that the chief genetic factor concerned may be undergoing quantitative variation. He rejects it on the ground that this explanation is not " in harmony with the results of Johannsen and other investigators." The work of Johannsen with seed-size in beans and the work of others with *Drosophila* is cited in support of this statement.

It is difficult to understand how the experiments of Johannsen have any direct bearing on the case since no single Mendelizing unit-factor was demonstrated in that connection; but in the hooded pattern of rats a Mendelizing unit-factor is unmistakably present and it is the quantitative variation of this which is under discussion, not the presence of many or few additional factors, concerning which Muller adopts our explanation. Appeal to the work of Johannsen with bean-size to show that our conclusions concerning color pattern in rats are incorrect is illogical because the cases are not parallel. The citation by Muller of the work on rabbit-size by MacDowell and myself[3] is equally non-germane, because no demonstrable Mendelizing unit-factor is involved in that case either. He might with propriety cite the bean work as bearing on the interpretation of the inheritance of body size in animals, or *vice versa*, since both involve blending inheritance. But neither of these cases has any direct bearing on the question of unit-character constancy, since in neither case has a unit-character, either constant or inconstant, been shown to exist.

The citation of work with *Drosophila* is more to the point, since the " mutations " of *Drosophila* Mendelize. But is it certain that they do not vary? Muller admits that they do *occasionally* vary, stating that " in one case (possibly in two or three cases)

[1] Castle and Phillips, ''Piebald Rats and Selection,'' Publ. No. 195, Carnegie Institution of Washington.

[2] AMER. NAT., Vol. 48, p. 567.

[3] Publ. No. 196, Carnegie Institution of Washington.

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a locus has mutated three times, each time in a different way.'' He does not think that smaller changes than these have occurred, since '' much smaller could easily have been detected.'' From this statement I infer that the opinion rests on casual inspection rather than measurement, for which reason I do not attach much importance to it. The hooded pattern of rats was not supposed to vary quantitatively until its quantitative study was undertaken. Two types of hooded rats were recognized, one more extensively pigmented than the other, and these were supposed to be discontinuous like the several '' mutations of a locus '' in *Drosophila.* Quantitative study has completely dispelled this idea as regards the hooded pattern of rats, and I have no doubt the same would be true of *Drosophila.* How easy it is to be sure of a thing which has not yet been investigated, so sure that investigation of it is considered a waste of time. Muller is confident that such variation as occurs in *Drosophila* '' can not even remotely be compared to fluctuating variability,'' and he generalizes thus:

> '' In no known case do the variations of a gene among, let us say, several thousand immediate descendants of the individual possessing it, form a probability curve.''

The use of the word '' gene '' in this sweeping statement safeguards the author, since no one, so far as I know, claims ever to have seen a '' gene '' or to have measured it. How could the '' variations of a gene '' be expected to '' form a probability curve '' if the gene is not measurable? But if the author will allow the substitution of *visible character* for '' gene '' in his challenge, I will gladly accept it and I will add this generalization for his consideration—*No one has by actual observation and measurement shown the existence of any visible character in any animal which is not quantitatively variable.*

As regards the mutations of *Drosophila* which Muller is confident (apparently without having studied the matter himself) do not vary so as to form a probability curve, I had sufficient curiosity some months ago to suggest a quantitative study by one of my pupils, Mr. D. H. Wenrich. Mr. Wenrich studied the wing-length of flies from a culture kindly supplied me by Professor Morgan under the name '' vestigial.'' In advance of a more detailed publication, Mr. Wenrich kindly permits me to state the following facts. The wing length measured in ocular micrometer units was found to vary as follows:

Classes	25–29	30–34	35–39	40–44	45–49
Frequencies	6	34	67	43	13
Classes	.50–54	55–59	60–64	65–69	
Frequencies	1	1	0	1	

The wing-length manifestly varies so as to form a pretty good probability curve; what the " gene " is doing, I do not undertake to say.

It is, of course, conceivable that the variation here observed in actual wing length might be due to variation in general body size, larger flies having longer wings. To determine this point measurements of tibia-length were made on the same flies, and in the case of each individual the ratio was computed between wing-length and tibia-length. These ratios are distributed as follows:

Ratios	.70–.79	.80–.89	.90–.99	1.00–1.09	1.10–1.19	1.20–1.29
Frequencies	2	7	26	49	47	23
Ratios	1.30–1.39	1.40–1.49	1.50–1.59	1.60–1.69	1.70–1.79	
Frequencies	7	3	0	0	2	

It is evident that there is no constant relation between wing-length and tibia-length, and so between wing-length and general size, with which tibia-length is closely correlated. Again we obtain a good probability curve. Does the " gene " vary or are we dealing also with additional modifying " genes "? We are confronted here with the same problem as in the case of the rats.

But it is possible to assume that the considerable variation shown by vestigial wings in *Drosophila* is purely somatic, " phenotypic," not due to genetic causes, and so would not show any effects if subjected to selection. So it was thought in the case of the plus and minus variations in the hooded pattern of rats, *before the experiment was made,* but experiment has shown, even to Mr. Muller's satisfaction, that the variations are in part due to genetic causes and that selection slowly and surely changes the range of variability. Is it safe to assume the contrary for *Drosophila* in the absence of all experiment?

Mr. Wenrich has also studied the wing-length of " extracted " vestigial flies obtained in the second generation from a cross between pure vestigials and normal flies, and he finds that the variability is regularly increased as compared with that of the uncrossed vestigial race. This again is parallel with what occurs when hooded rats are crossed with wild or with Irish rats, and indicates that similar causes are at work in the two cases. Such

cases present to the genotype theory the following dilemma. Either *one* gene is concerned in the case or many genes. If one only is concerned, it is variable. If many genes are concerned, they are so numerous (whether or not constant) that they present to the observer of the visible character affected a continuous variation series, one capable of indefinite displacement up or down the quantitative scale. The supposed distinction between continuous and discontinuous variation then vanishes. Selection in that case meets with no " *fixed limit* " beyond which it cannot go.

Mr. Muller is seriously disturbed (p. 573) because we are willing to consider it possible that the " factor for hooded " may be contaminated by " its allelomorph (the factor for self) " while associated with it in the zygote represented by the F_1 rats. (The evidence of modification is unmistakable, however one attempts to explain it.) He says this is " violating one of the most fundamental principles of genetics—the non-mixing of factors— in order to support a violation of another fundamental principle—the constancy of factors." Now, when, I should like to inquire, did these principles become " fundamental "; by whom were they established and on what evidence do they rest? I should suppose that Bateson, president of the British Association, might be considered fairly well posted on the " principles of genetics," but neither in his earliest papers nor in his latest do we find any mention of these sacred principles. In his recent presidential address[4] he frankly states his belief that segregation is often imperfect and that " fractionation " of factors frequently occurs as a result of crossing.

We shall look in vain, I think, for those " principles " outside of the "Exakten Erblichkeitslehre" (or its imitations), and when we inquire as to the experimental basis of the principles in question we are met with the satisfied reply, "Johannsen's beans." What a slender basis and what and absurd one from which to derive the " fundamental principle " that Mendelian factors are constant! Yet to date this case, which admittedly involves no clear Mendelian factor, is the only evidence worth mentioning in favor of the constancy *of Mendelian factors!* Do biologists take themselves seriously when they reason thus? Certainly no one else will long take them seriously.

Finally, I may be permitted to correct two misapprehensions

[4] *Science,* August 28, 1914.

into which Muller in common with the Hagedoorns[5] has fallen, viz., (1) that individual pedigrees were not recorded in the course of our selection experiments and (2) that no considerable amount of inbreeding occurred in our work.

It has been our invariable practise, upon recording the birth of an animal and its grade, to record on the same line of the ledger the record number of its mother and father. This enables one in any particular case to trace back the pedigree to the very beginning of our experiments. We have spent much time writing out and studying individual pedigrees, but without discovering any evidence of pure or prepotent lines or individuals, except in a single case, that of our "mutant" series, the origin and complete history of which we have described in detail. The pedigrees, however, of our rats are on record available for study at any time; their full publication would be a quite impossible undertaking.

That extensive and intensive inbreeding has occurred in our experiments will be obvious when I state that all our animals were descended from a very small initial stock, less than a dozen individuals, that from the beginning we have made the most extreme selections possible, mating like with like, never hesitating to mate brother with sister, and putting aside for strict brother-sister matings any litter of young which seemed especially promising. I may say that in no single case (except that of the "mutant" series) have these "special" pens given us advancement obviously greater or less than that of the general selection series of which they formed a part. Nevertheless, we are still continuing to follow them up and will later publish a detailed account of them. Finally I would call attention to pp. 20 and 21 with Tables 48–49 of our full publication, in which are described the hooded offspring of a single selected hooded and a single wild rat. The hooded and the wild rat produced several young resembling the latter, that is, not hooded; these were mated *inter se,* brother with sister. Among the grandchildren (F_2) occurred the usual 25 per cent. of recessives, hooded. Two males were selected from these and mated with females of as nearly the same grade as were available. This process was repeated through seven generations in succession. Seven times animals of like grade were mated together, brother

[5] *Zeit. f. ind. Abst. u. Vererbungslehre,* 11, p. 145. See also my reply in the same journal, 12, p.

with sister when possible, less often brother with half-sister, rarely cousin with cousin. In this way were obtained 804 young from rigidly selected, closely inbred descendants of a single pair of rats, the series extending into generation F_8. We have shown (*l. c.*, p. 21) that the progress of selection within this inbred family follows a remarkably close parallel, generation by generation, to the progress of selection in our plus series as a whole. Muller's anticipation that a different result would follow close inbreeding is not justified by our observations.

In discussing this experiment (p. 21) we have italicized the statement that (so far as the hooded character is concerned) *the entire series is derived from a single hooded individual!* When the Hagedoorns made the statement that our stock had not been sufficiently inbred, they had apparently not seen our full publication and so had no means of knowing to what extent it had been inbred, but Muller, with our full publication before him, apparently repeats the statement without taking the trouble to verify it.

W. E. Castle

Bussey Institution,
    October 23, 1914

NO CROSSING OVER IN THE FEMALE OF THE SILKWORM MOTH

In a recent review[1] of a paper by Y. Tanaka[2] on linkage in the silkworm moth, I pointed out that some of his data suggested that crossing over was occurring in only one sex. While the data were not sufficient to establish this conclusion, there was at this time another paper by the same author[3] which I had not seen. In this paper are presented data which clear up the matter.

Tanaka has now made back-cross tests of both sexes. That crossing over does occur in the males was shown by the mating sysy ♀ × SYsy ♂, which gave a total of 865 cross-overs among 2,907 offspring. The cross sysy ♀ × SysY ♂ gave 151/488 as the proportion of cross-overs. But when females were tested, SYsy ♀ × sysy ♂ gave no cross-overs in 1,183 offspring. Tanaka refers to another paper, apparently in press, in which he has shown the same relations (*i. e.*, crossing over in males, none in

[1] Amer. Nat., XLVIII, 1914.
[2] *Jour. Coll. Agr. Tohoku Imp. Univ. Sapporo*, V, 1913.
[3] *Jour. Coll. Agr. Tohoku Imp. Univ. Sapporo*, VI, 1914.

females) for the combinations NynY and MYmy. As stated in my former review, there was in the earlier paper a record of the mating sysy ♀ × SysY ♂, giving no cross-overs in 128 offspring. Tanaka now says, referring to this case: ''Whether there may exist, in certain occasion, a complete reduplication [linkage] in *male*, or whether the above result is due to any mistake by which sex-signs have been reversed, is at present uncertain. No similar case has as yet been found in other families.''

The evidence seems to make it highly probable that crossing over in the silkworm moth occurs only in the male; a surprising result when we remember that in *Drosophila* it occurs only in the *female*. One is immediately reminded that in *Drosophila* the male is heterozygous for the sex-differentiator, while in *Abraxas* and probably all moths the female is the heterozygous sex. These facts are highly suggestive, and lead one to wonder what will be found with regard to crossing over in the two sexes in birds and mammals, where similar differences in sex-determination occur. Another point worth noting in this connection is that in the hermaphroditic sweet pea and *Primula* crossing over occurs in the formation both of pollen and of ovules.

Tanaka reports two cases of aberrant results which, as he says, may be explained as due to mutation (''dropping out'') of S in one case, and of both S and Y in the other. He adds that such an assumption is premature. To the writer it seems more probable that the females involved were not virgin. The results are easily explained on the assumption that they had paired with brothers before isolation, since brothers of the necessary composition are shown by the pedigrees to have been present in each case.

Another interesting point brought out by Tanaka's more recent paper is the relation between the larval patterns known as striped, moricaud, normal, and plain. In my earlier review I followed Tanaka in treating these patterns as affected by three pairs of genes: S (striped) and s, M (moricaud) and m, and N (normal) and n, plain being the triple recessive. The same scheme has been followed in the early part of this paper. On this assumption, as Tanaka points out, it is necessary to suppose that complete linkage occurs between these three pairs of genes. The evidence need not be gone over in detail here, but there are over 10,000 larvæ recorded from various tests of this relation, without a single cross-over among them. Although Tanaka does not mention the point, this at once brings up the possibility that

we may be dealing with a system of multiple allelomorphs. No two of the types when mated together give a third in F_1; and, unless one or both carry a recessive in heterozygous form, any two types give a 3 : 1 ratio in F_2, or 1 : 1 on back-crossing to a recessive. The four patterns involved seem, from the descriptions, to fall roughly into a series in the order striped, moricaud, normal, and plain. That is to say, the second two are rather intermediate in appearance between striped and plain. Although I believe any arguments as to the nature of genes which are based on the appearance of characters are open to very serious objections, it must still be admitted that the different characters involved in a case of multiple allelomorphism are generally of the same sort.[4]

On the chromosome view, if the genes just discussed are allelomorphs they occupy identical loci in homologous chromosomes. If they are not allelomorphic but closely linked, they occupy different but closely opposed loci in homologous chromosomes. In either case, any combination of them should give approximately the same linkage to the Y–y pair of genes, which occupy a locus in the same chromosome, but some distance away. The linkage of the striped-normal, striped-plain, and moricaud-plain combinations with the Y–y locus appear from Tanaka's data to be in fact about the same, though the data on the first (striped-normal) are the only ones sufficiently large to be very significant.

A. H. STURTEVANT

COLUMBIA UNIVERSITY,
    October, 1914

THE INFLUENCE OF POSITION IN THE POD UPON THE WEIGHT OF THE BEAN SEED

IN a note on the pure line problem Belling[1] has emphasized the significance of position in the pod as a factor in determining the weight of the bean seed. Since this point in his paper seems to have attracted some attention among those interested in genetics, it may not be out of place to call attention to a series of quantitative determinations of the intensity of the relationship[2] and to illustrate the results secured.

If one numbers the successive ovules of the pod from 1 up,

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[4] I have discussed this aspect of the matter briefly in another paper (AMER. NAT., XLVII, 1913, p. 237).

[1] Belling, J., "Selection in Pure Lines," *Amer. Breed. Mag.*, 3: 311–312, 1912.

[2] Harris, J. Arthur, "A Quantitative Study of the Factors Influencing the

he may regard the numbers as measures (in units of intervals between adjacent ovules) of the distance of ovules from the
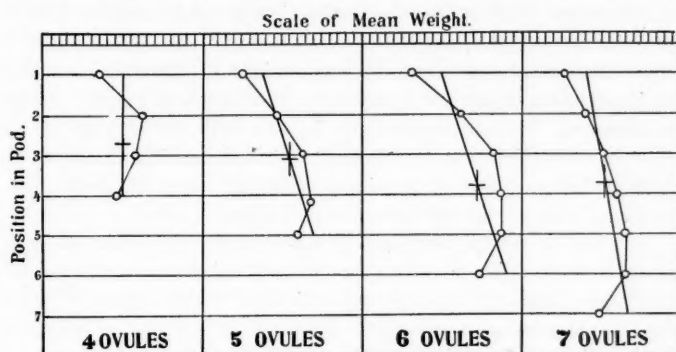
Scale of Mean Weight.

Fig. 1.

proximal end of the pod, and may then express in terms of correlation the relationship between the weight of the seed and its position in the pod.

Scale of Mean Weight.
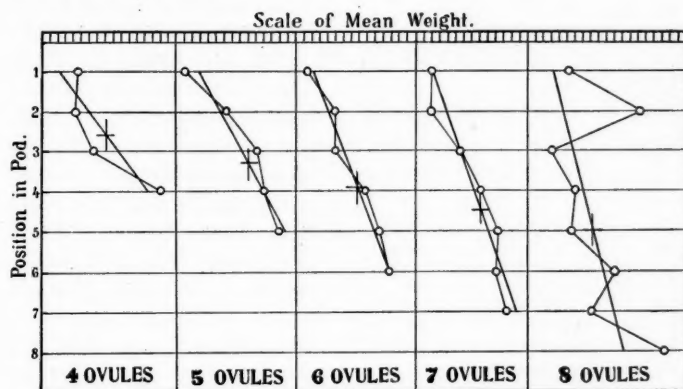
Fig. 2.

In doing this, the pods should of course be sorted into classes according to the number of ovules which they produce and the relationship computed for each group of pods separately, for there is no reason for believing that the fourth in a pod with 4 ovules is comparable with the fourth seed in a pod with six. This

Weight of the Bean Seed. I. Intra-Ovarial Correlations,'' *Beih. Bot. Centralbl. Abt.*, I, 31: 1–12, Pl. 1–4, 1913.

has now been done for twenty series of pods, drawn from five cultures belonging to three distinct varieties (Navy, Golden Wax and Burpee's Stringless) and embracing altogether about 23,000 individually weighed seeds. In every one of these cases a positive correlation has been found, *i.e.*, the weight of the seed increases as its distance from the base of the pod becomes greater. The intensity of this interdependence is, however, not very great, at least in the varieties so far studied. The correlations range from .014 ± .046 to .238 ± .068, with an average value of about .132, or about 13 per cent. of perfect correlation.

The rate of change has been expressed by the slope of a straight line for four different classes of pods studied for a culture of Navy beans made at Sharpsburg, Ohio, in 1907 (Diagram 1[3]) and for five classes from a culture of Burpee's Stringless beans grown at the Missouri Botanical Garden in the same year.

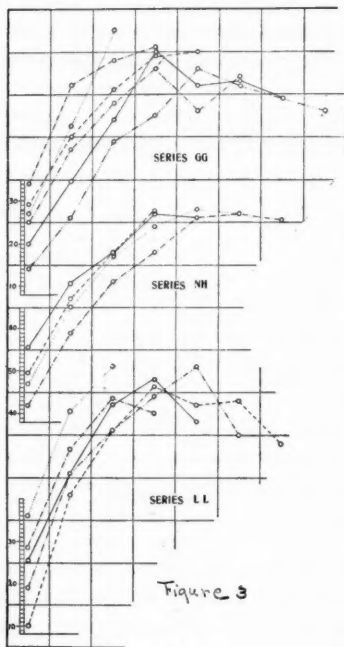SERIES GG

SERIES NH

SERIES LL

Figure 3

FIG. 3.

In the first of these, the Navy series, it appears that the observed mean weights at first increase rather rapidly, then the rate of increase falls off and finally the seeds nearest the tip (distal or "blossom" end of the pod) become somewhat lighter than those a little lower down. Here a curve would fit the observed means better than a straight line. In the Burpee's Stringless culture (Fig. 2) however, the change in seed weight can for all practical purposes be represented by a straight line as well as by any curve.

The percentage of ovules which develop into seeds also increases from the base toward the stigmatic end of the pod. In small pods the rate of increase may be fairly regular, but in larger pods

[3] In the diagram for this series published in the original paper there is a slip in the representation of the slope of the line for pods with 4 ovules.

it falls off toward the stigmatic end, where the fecundity may be even lower than it is a little farther down in the pod. This is admirably shown in Diagram 3, in which *GG* stands for a series of Burpee's Stringless grown at the Missouri Botanical Garden, *NH* for a series of Navy beans grown at Sharpsburg, Ohio, and *LL* for a series of Golden Wax beans grown at Lawrence, Kansas. All were grown in 1907. Here the percentage of development of ovules at different positions in the pod is shown for the different classes of pods by the scales to the left of the figures. The reader may ascertain the class of pods represented by any particular curve by noting the number of circles representing percentage development in the various positions. These correspond to the number of ovules per pod. In the diagrams the positions (abscissæ) from left to right represent the positions from the base to the tip of the pod.

<div style="text-align:right">J. Arthur Harris</div>

ANOTHER GENE IN THE FOURTH CHROMOSOME OF DROSOPHILA

Until the appearance of bent wings, only three groups of linked genes had been found in *Drosophila amelophila*, although four pairs of chromosomes had been identified in the diploid group. Since the character bent wings, worked out by Mr. H. J. Muller, was found to be unassociated with any of the three groups, the gene producing this character was said to be located in the fourth chromosome.

Recently a new character, designated as eyeless, appeared. Flies having this character either lacked eye pigment and ommatidia or had one or both eyes reduced in size. All of the pure stock showed some loss of eye structures. Eyeless is recessive to the normal eye. In order to determine the linkage, eyeless males were crossed in turn to females of the stocks at Columbia University. These stocks representing the three groups were (1) miniature wings, (2) black body and vestigial wings, and (3) spread wings. The genes producing these characters are in the first, second and third chromosomes, respectively. The F_1 from all three crosses had normal eyes. They were inbred in each case and gave the following.

The equation should be $w = 9.987 + .021\ p$. The line as it appears here is correctly drawn.

<div align="center">Cross 1.   Miniature ♀ by Eyeless ♂</div>

F_2.	Normal Long	Normal Miniature	Eyeless Long	Eyeless Miniature
	1142	1106	245	193

Since the eyeless flies were females as well as males, the character eyeless is shown not to be a sex-linked character; for, if it were, it would be inherited only by the grandsons of the eyeless male. Since the eyeless flies are not nearly as viable as the wild stock, the eyeless classes fall below the expectation.

<div align="center">Cross 2.   Black Vestigial ♀ by Eyeless ♂</div>

F_2.	Normal Long	Normal Vestigial	Eyeless Long	Eyeless Vestigial
	1303	417	278	97

The same count, when grouped according to the body color, was as follows:

F_2.	Normal Gray	Normal Black	Eyeless Grey	Eyeless Black
	1289	431	293	82

<div align="center">Cross 3.   Spread ♀ by Eyeless ♂</div>

F_2.	Normal not Spread	Normal Spread	Eyeless not Spread	Eyeless Spread
	1349	373	300	76

Allowing for the decreased viability of eyeless, both of the preceding crosses may be regarded as $9:3:3:1$ ratios. Hence they show that there is no linkage of eyeless with the characters whose genes are in the second and third chromosomes.

Eyeless females were then crossed to bent-winged males (Cross 4). No bent eyeless flies were produced in the F_2. As the count was small, the F_2 bent flies were crossed to the F_2 eyeless, and then the F_3 normal, which had the same germinal constitution as the F_1, were inbred to give F_4, which should give the same results as the F_2.

<div align="center">Cross 4.   Bent ♂ by Eyeless ♀</div>

	Normal not Bent	Normal Bent	Eyeless not Bent	Eyeless Bent
F_2.	596	193	195	0
F_4.	741	172	131	0
Total	1337	365	326	0

Since an approximate $2:1:1:0$ ratio, instead of a $9:3:3:1$ ratio, was realized, the conclusion that eyeless and bent belong

to the same group and in this sense may be said to be in the same chromosome pair is evident. Until a bent eyeless fly—a cross over—is obtained, the amount of crossing over between these two characters in the fourth chromosome can not be directly determined.

MILDRED A. HOGE

AN ABNORMAL HEN'S EGG

IN a frequently quoted paper, Parker ('06) has classified double eggs on the basis of the factors supposedly concerned in their formation. Considering the ovarian and oviducal factors as independent, Parker says:

As a result of these two factors, three classes of double eggs can be distinguished; first, those whose yolks have come from an abnormal ovary but have passed through a normal oviduct; secondly, those whose yolks have come from a normal ovary but have passed through an abnormal oviduct; and finally those produced by an ovary and oviduct both of which have been abnormal in their action.
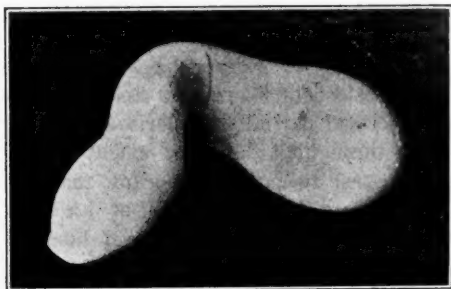

FIG. 1.   PHOTOGRAPH OF THE SPECIMEN × 1.

Cases of ovum in ovo have been attributed by Parker and others to antiperistalsis. Patterson ('11) mentions a case of an inclosed double egg in which there were two distinct peristaltic actions. Féré ('98) has called attention to the fact that hens frequently lay several double eggs in succession. Féré claims that he succeeded in producing double eggs in a hen which normally laid single eggs, by drugging her with atropine sulphate. Glaser ('13) has described the ovary of a hen which habitually laid double eggs and concludes that fusion of the follicles is the explanation of some double eggs.

The case which I wish to record is very similar to that figured by Hargitt ('12) and termed by him a "gourd-shaped" egg. Unfortunately, the egg which Professor Hargitt studied was not preserved carefully and on account of evaporation, the condition was such that he could not be certain of the presence of yolk in the smaller end. He assumed that the egg was comprised of
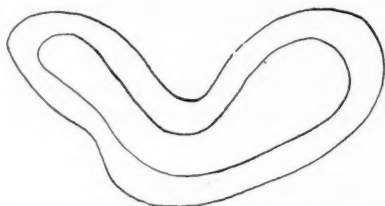
Fig. 2. Diagrammatic Mesial View of the Abnormal Egg, Showing the Relation of the Yolk to the Albumen.

about normal parts in the larger end, and that the smaller consisted of only albumen, "its yellowish tint having resulted from the evaporating process which had taken place."

The egg shown (Fig. 1) was presented to Professor Julius Nelson, of Rutgers College, several years ago and was carefully preserved in a jar of alcohol. The result was that although the action of the alcohol had partially decolorized the yolk, it was possible to trace it throughout the entire extent with no difficulty. As can be readily seen from the photograph, that part of the egg which might be termed the "neck" presented a much roughened appearance from the excessive accretion of lime. A nodule of lime at the smaller end of the shell would seem to indicate that the last deposit of the shell glands was there received.

For convenience in examination of the irregular shaped egg, it was separated at the circling line seen in Fig. 1, and then the two parts were halved with a sharp scalpel, after the penetration of the shell by means of scissors.

When the first separation was made at the line indicated, one could readily discern the presence of a *constricted* yolk surrounded by apparently normal albumen. Examination of the halved portions showed that the yolk extended from the larger end through the constricted region to occupy a position approximately normal in the smaller end. It seems possible that this particular abnormality may have been caused by a constricted

oviduct rather than from the fusion of two eggs during apposition, induced by anti-peristalsis.[1]

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[1] Since the above was written, but before the proof came to hand, an authoritative paper has been published (Maynie R. Curtis, Studies on the Physiology of Reproduction in the Domestic Fowl, Vi. Double- and Triple-Yolked Eggs. Biol. Bull. Vol. 26, pp. 55–83.) in which no mention has been made of the possibility of incomplete separation of both yolk and albumen of a single egg. Evidence of such separation is not wanting in other vertebrates, however scant it may be in the fowl.

SCIENTIFIC LITERATURE

GENETIC DEFINITIONS IN THE NEW STANDARD DICTIONARY

THE widely advertised aim of the Funk & Wagnalls Company to include in their "New Standard Dictionary of the English Language " all of the new additions to scientific terminology naturally invites the specialist in each branch of science to examine the definitions of the new words in his own field. Professor Miller[1] has called attention to the fact that the mathematical definitions are not reliable. The same criticism must be made regarding the definitions of many terms now familiar in the literature of genetics. For some of the errors in these definitions the editorial staff can not be blamed, because the errors were passing current among genetic writers themselves, at a time when further changes in the dictionary probably became impossible; other errors are less easily explained. While such a monumental work as the Standard Dictionary tends to fix the usage of language, the shortcomings of the genetic definitions may not be expected to seriously affect the terminology actually used by the specialists in this field; but for those who are engaged in other scientific fields, who have only a casual interest in genetics, and who must, therefore, depend upon the dictionary for the meaning of any genetic terms they may happen to meet, the erroneous definitions are unfortunate. While very few of the genetic definitions are free from defects, either of omission or of commission, only those which seem most obviously defective will be considered here. In the following list of words the definition of the New Standard Dictionary is stated first, and then follows, in italic type, a definition which I believe will meet with the approval of most geneticists.

Acquired. Transmitted by inheritance to subsequent generations; as, *acquired* characters.

Acquired character. *A modification of bodily structure or habit which is impressed on the organism in the course of individual life.*

Both of these definitions occur in the New Standard Dictionary, the first under "acquired," the second under "character." Although "impressed on" may not be the best figure of speech to use in this connection, the second definition represents fairly well the correct usage of this phrase. It is difficult to understand why

[1] *Science*, N. S., 38: 772, November 28, 1913.

essentially the same definition should not have been given at both places.

Allelomorph. "In Mendelian inheritance a pair of contrasted characters which become segregated in the formation of reproductive cells."

Allelomorph. *One of a pair of contrasted characters which are alternative to each other in Mendelian inheritance. Often used with doubtful propriety as a synonym for gene, factor or determiner.*

The defects in the dictionary definition in this case are two: (*a*) The definition is plural, while "allelomorph" is singular; the "allelomorph" is not a *pair* of characters, but a *single* character. (*b*) No segregation of allelomorphs takes place in the formation of asexual reproductive cells.

Allelomorphism. "The presence of allelomorphic pairs of characters."

Allelomorphism. *A relation between two characters, such that the determiners of both do not enter the same gamete, but are separated into sister gametes.*

Alternative inheritance. "The transmission to alternating generations of descendants of the characteristics of either parent, as that of the father to the odd, and of the mother to the even generations."

Alternative inheritance. *A distribution of contrasting parental or ancestral characters among offspring or descendants, such that the individuals exhibit one or other of the characters in question, combinations or blends of these characters being absent or exceptional.*

Biotype. "In Mendelian inheritance a race or strain that breeds true or almost true; a term introduced by Johannsen."

Biotype. *A group of individuals all of which have the same genotype.*

The word "biotype" was introduced into English by Dr. Johannsen[2] in 1906 with the definition "one single 'sort' of organisms." It is a term of general applicability and not limited to Mendelian races, as stated in the New Standard Dictionary. Although homozygous biotypes generally do breed true, this is not an essential feature and therefore should not be included in the definition. Ever-sporting varieties are now well known which do not breed true, but which, so far as present evidence goes, do constitute single homozygous biotypes. Heterozygous biotypes generally do not breed true.

Clon. "A plant-group the members of which have been grown from an original stock, but which do not come true from seed."

Clone. *A group of individuals produced from a single original individual by some process of asexual reproduction, such as division, budding, slipping, grafting, parthenogenesis (when unaccompanied by a reduction of the chromosomes), etc.*

There are several defects in the dictionary definition of this word, even if restricted to a plant-group in accord with the original meaning given to it by Webber, who introduced the word.

[2] Report of the third International Conference of Genetics, p. 98.

The defects consist, first, in the ambiguity of the word "stock," because we may grow plants "from an original stock" of seeds, quite as well as from cuttings, while a clone is derived from a single individual; second, the statement that clones do not come true from seed is incorrect, for a clone formed by cuttings, etc., from a homozygous individual does "breed true," *i. e.*, it produces seedling offspring of its own type. The word is now being generally applied to animals as well as to plants.

Coupling. ("Genetic coupling" is not defined in the dictionary.) *Such a relation between the genes of two unit-characters that they have a more or less marked tendency to be included in the same gamete when the individual is heterozygous for both of the genes in question.*

Cross-over. (Not given a genetic definition in the dictionary.) *A separation into different gametes, of determiners that are usually coupled, and the association of determiners in the same gamete, which are generally allelomorphic.*

Cryptomere. "A plant character which may exist in the germ-cells without making its presence visible."

Cryptomere. *A factor or gene whose presence can not be inferred from an inspection of the individual, but whose existence can be demonstrated by means of suitable crosses.*

The chief defect in the dictionary definition is the restriction of this term to *plant* characters. "Cryptomere" is a general genetic term which may be applied as well to animals as to plants.

Determiner. "The same as determinant 3."

Determiner. *An element or condition in a germ-cell which is essential to the development of a particular feature, quality or manner of reaction of the organism which arises from that germ-cell; a gene or factor.*

The word "determiner," as used in recent years, is not the equivalent of "determinant 3," which latter is correctly defined in the dictionary in terms of Weismann's complicated hypothesis. "Determiner," "factor" and "gene" are now quite generally used interchangeably without implication as to their fundamental nature, simply in the generic sense, as "that which determines."

Dominance. "In the cross-bred offspring of parents with marked mutually antagonistic characteristics, the exhibition by such offspring or its descendants of one of these characteristics to the exclusion of the other."

Dominance. *In Mendelian hybrids the capacity of a character which is derived from only one of the two generating gametes to develop to an extent nearly or quite equal to that exhibited by an individual which has derived the same character from both of the generating gametes. In the absence of dominance the given character of the hybrid usually presents a "blend" or intermediate conldition between the two parents, but may present new features not found in either parent.*

There are several defects in the dictionary definition. In the first place, the parents used in a given cross may not themselves

be homozygous, in which case some of their offspring will resemble one parent and some the other; in such a case, according to the dictionary, both of the contrasted characters would exhibit dominance. The phrase ''or its descendants'' would make it possible, *in any case,* to include both recessives and dominants, since among the *descendants* of such cross-bred individuals there will also be *recessive* individuals which ''exhibit one of the characteristics to the exclusion of the other.''

Dominant. '' (1) A marked parental character exhibited by a cross-bred organism and its descendants. (2) The parent, cross-bred organism, or descendant exhibiting such character. Parental characters latent in a cross-bred organism, but actively evidenced by its descendants, are called *recessives,* as are the descendants which exhibit them.''

Dominant. *(1) A character which exhibits dominance, i. e., that one of two contrasted parental characters which appears in the individuals of the first hybrid generation to the exclusion of the alternative, ''recessive,'' character. (2) An individual possessing a dominant character, in contrast to those individuals which lack that character, which are called ''recessives.''*

An ''*extracted* dominant,'' as defined in the dictionary, is not distinguishable from the pure homozygous dominant used in the cross from which the dominant in question was ''extracted,'' as no mention is made of the essential historical fact that it is of hybrid origin and that its parent or other known ancestor did not breed true to the same dominant character.

Factors. ''Latent physiological units which upon crossing give rise to the new characters found in the hybrid.''

Factor. *An independently inheritable element of the genotype whose presence makes possible any specific reaction or the development of any particular unit-character of the organism which possesses that genotype; a gene or determiner.*

The limitation of the term ''factor'' to those cases in which new characters appear in hybrids, is not in accord with present usage. All the various characters of organisms are to an important degree dependent upon the existence of genotypic factors, regardless of the behavior of these organisms in crosses.

Gen. ''A minute hypothetical particle supposed to be the bearer of hereditary qualities.''

Gene. *An element of the genotype; a genetic factor; a determiner.*

The treatment of this word in the dictionary is particularly mischievous. When I introduced the word ''gene'' to English-reading students, I said:[3] ''This word is proposed by Dr. Johannsen . . . to denote an internal something or condition upon whose presence an elementary morphological or physiological characteristic depends. The word 'gene' has the advan-

3 AM. NAT., 43, p. 414, 1909.

tage that it does not assume by its form or derivation any hypoth-
esis as to the ultimate character, origin or behavior of the deter-
mining factor.''   In adopting the word ''Gen'' in the German,
Johannsen said:[4] ''Das Wort *Gen* ist völlig frei von jeder Hy-
pothese; es drückt nur die sichergestellte Tatsache aus, dass jeden-
falls viele Eigenschaften des Organismus durch in den Gameten
vorkommende besondere, trennbare und somit selbständige
'Zustände,' 'Grundlagen,' 'Anlagen'—kurz, was wir eben *Gene*
nennen wollen—bedingt sind. . . . die Gene sehr vieler Eigen-
schaften glatt trennbar sind, während andere nicht oder nicht
glatt sich trennen.   Dies alles erinnert an das Verhalten chemi-
scher Körper.   Damit ist aber noch gar nicht gesagt, dass die Gene
selbst chemische Gebilde oder Zustände seien—darüber wissen
wir vorläufig noch gar nichts.''   How different is all this from ''a
minute hypothetical particle''!   It is obviously improper, there-
fore, to define a gene as a ''minute particle.''   Neither is it correct
to say that it is ''supposed to be the bearer of hereditary qual-
ities.''   It is only the something of unascertained nature, which
must lie at the foundation of any elementary hereditary quality.
The spelling ''gene'' is not even mentioned in the dictionary as a
variant, yet this was the original spelling and is now in practic-
ally universal use among geneticists, while no one uses ''gen.''

Genotype. ''A race of organisms different from another in its hereditary
qualities; contrasted with *phenotype.*''

Genotype. *The fundamental hereditary constitution or sum of all the
genes of an organism.*

The unfortunate definition of ''genotype'' given in the dic-
tionary was current in America at the time when the dictionary
forms were probably closed, so that the editors are not in any way
to blame for the totally erroneous definition.   The definition given
by the dictionary for ''genotype'' fits fairly well the word
''biotype.''

Heredity. ''The tendency manifested by an organism to develop in the
likeness of a progenitor.''

Heredity. *The distribution of genotypic elements of ancestors among
the descendants; the resemblance of an organism to its parents and other
ancestors with respect to genotypic constitution.*

The results of modern experimental work on heredity show that
the definition given by the dictionary is entirely too restricted.
Heredity must be so defined that it may apply to characters that
were never exhibited by any ancestor.

Heterozygosity. ''In Mendelian inheritance, the state or condition due
to an organism having developed from a heterozygote.''

[4] ''Elemente der exakten Erblichkeitslehre,'' 1. Aufl., 1909, pp. 124–125.

Heterozygosity. *The condition of an organism due to the fact that it is a heterozygote; the state of being heterozygous; the extent to which an individual is heterozygous.*

Heterozygote. "A Mendelian hybrid resulting from the fusion of two gametes that bear different allelomorphs of the same character and which in consequence does not breed true; contrasted with *homozygote.*"

Heterozygote. *A zygotic individual in which any given genetic factor has been derived from only one of the two generating gametes. Both eggs and sperms produced by such an individual are typically of two kinds, half of them containing the gene in question, the rest lacking this gene; consequently the offspring of heterozygotes usually consist of a mixture of individuals, some of which possess the corresponding character while others lack it.*

Homozygosis. "Development from a zygote originating from a union of two gametes of the same kind."

Homozygosis. *The state of being homozygous; the extent to which an individual is homozygous.*

Homozygote. "A zygote formed by the conjugation of two gametes of the same stock; any animal or plant that receives and retains the dominant or recessive characters of both its parents, and is therefore said to be true to type, and breeds true to type."

Homozygote. *An individual in which any given genetic factor is doubly present, due usually to the fact that the two gametes which gave rise to this individual were alike with respect to the determiner, in question. Such an individual, having been formed by the union of like gametes, in turn generally produces gametes of only one kind with respect to the given character, thus giving rise to offspring which are, in this regard, like the parents; in other words, homozygotes usually "breed true." A "positive" homozygote with respect to any character contains a pair of determiners for that character, while a "negative" homozygote lacks this pair of determiners.*

"Two gametes of the same stock" is ambiguous because of the indefiniteness of the word "stock." Many homozygotes receive some dominant *and* some recessive characteristics of the two parents; and what can be intended by the statement that a plant or animal which receives certain characteristics also *"retains"* them? How could it do otherwise?

Hypostasis. (Not given a genetic definition in the dictionary.) *That relation of a gene in which its usual reaction fails to appear because of the masking or inhibitory effect of another gene; contrasted with "epistasis."*

The corresponding adjective "hypostatic" is also not given a genetic definition in the dictionary.

Mendelize. "To cause to follow Mendel's law of inheritance."
Mendelize. *To follow Mendel's law of inheritance.*

The word is rightly indicated in the dictionary, as an intransitive verb; it is manifestly incorrect to define it by the use of a transitive verb.

Mutant. ''That which admits of or undergoes mutation or change; specifically, an individual or a species which shows significant changes in form or character in a single generation.''

Mutant. *An individual possessing a genotypic character differing from that of its parent or those of its parents, and not derived from them by a normal process of segregation.*

The expression ''significant changes'' is ambiguous, since every change is significant of something.

Mutate. ''To 'sport.' ''

Mutate. *To undergo a change in genotypic character independently of normal segregation.*

The word ''sport'' which is used in the dictionary definition of ''mutate'' is defined thus: ''To vary suddenly or spontaneously from the normal type; said of an animal or plant or of one of its parts.'' It is well known that many such sudden and spontaneous variations from the normal type are not due to mutations. The word ''mutation'' is defined in the dictionary as ''a permanent transmissible variation in organisms, as distinct from *fluctuation.*'' This definition is good as far as it goes, but should expressly exclude transmissible variations which are due to normal segregation and recombination of determiners.

Phenotype. ''A type or strain of organisms distinguishable from others by some character or characters, whether their observable differences from other organisms be due to their inherent hereditary differences or to the direct action of the environment upon them: contrasted with *genotype.*''

Phenotype. *The apparent type of an individual or group of individuals,* i. e., *the sum of the externally obvious characteristics which an individual possesses, or which a group of individuals possesses in common; contrasted with genotype.*

''Phenotype'' and ''genotype'' are both abstractions; the qualities which distinguish the phenotype are always capable of direct observation, while those of the genotype can only be inferred from the results of genetic experiments.

Presence and absence hypothesis, ''in the Mendelian doctrine of inheritance, the theory that an allelomorphic pair of characters in every zygote has two contrasted factors or determinants, one representing the positive character of the generated organism and the other denoting its absence.''

Presence and absence hypothesis. *The hypothesis that any simple Mendelian difference between two individuals, results solely from the presence of a factor in the genotype of the one individual, which is absent from that of the other. Presence and absence of unit-differences as a convenient* method *of describing the results of genetic experiments should be carefully distinguished from the presence and absence* hypothesis. *The* method *is purely objective and entirely free from hypothetical implications.*

It will be noted that the dictionary definition of this phrase is directly opposite in significance to the one here set forth.

Pure line (Not included in the dictionary.) *A group of individuals derived solely by one or more self-fertilizations from a common homozygous ancestor. Sometimes erroneously applied to groups of individuals believed to be genotypically homogeneous (a homozygous biotype or a clone) without regard to their method of reproduction.*

Repulsion. (Not given a genetic definition in the dictionary.) *Such a relation between two genetic factors that both are not, as a rule, included in the same gamete, referring especially to cases in which the factors in question give rise to obviously different characteristics; also called "spurious allelomorphism."*

Sex-limited inheritance. (Not defined in the dictionary.) *The association of the determiner for any unit-character, with a sex-determiner, in such a manner that the two determiners are either generally included in the same gamete, or that they are generally included in different gametes. This method of inheritance is also called "sex-linked" inheritance by Professor T. H. Morgan and his students.*

Segregate. "To become separated from the rest; specif., of Mendelian hybrids, to separate, by a numerical law, into dominants, hybrids and recessives."

Segregate. *With reference to Mendelian unit-characters, to become separated through the independent distribution of the genetic factors before or at the time of the formation of the gametes.*

The dictionary definition goes too far; the formation of dominants, hybrids and recessives depends not alone upon the fact that the factors *segregate,* but that the segregated factors *recombine.* The word "segregation" receives a fairly satisfactory definition.

Unit-character. (Not included in the dictionary.) *In Mendelian inheritance a character or alternative difference of any kind, which is either present or absent, as a whole, in each individual, and which is capable of becoming associated in new combinations with other unit-characters.*

I have made no systematic study of the definitions of technical terms in other related fields, but have noted incidentally that there is no recognition in the New Standard Dictionary of the generally familiar usage of the words "meristic" and "substantive" as applied to types of variation.

<div align="right">G. H. Shull</div>

PROFESSOR DE VRIES ON THE PROBABLE ORIGIN OF ŒNOTHERA LAMARCKIANA

In a recent paper Professor Hugo De Vries[1] has given us the results of a second examination in 1913 of material from the herbarium of Lamarck, and of other sheets of *Œnothera* in the collections of the Muséum d'Histoire Naturelle in Paris. This

[1] De Vries, Hugo, "The Probable Origin of *Œnothera Lamarckiana* Ser., *Bot. Gaz.,* Vol. LVII, p. 345, 1914.

is a very important contribution for there have been some changes in the mounting of important specimens in the herbarium of Lamarck since the first studies by De Vries in 1895 and it was not clear what material formed the subject of his discussion in "Die Mutationstheorie." As the result of this second examination (1913) there can be no misunderstanding of De Vries's conclusion as to what represents the type of *Œnothera Lamarckiana* Seringe, and we have also very positive opinions on the identity of other interesting material in the collections at Paris. Thanks to his descriptions and photographs of these sheets further confusion will be impossible and botanists may now make for themselves the observations that will in the end determine their judgment of the soundness of Professor De Vries's views and of the value of the exceptions that may be taken to them.

I shall not at this time discuss in detail the queries which presented themselves on my reading of De Vries's paper. The most important of the points probably rest on facts that should be shown by the material, but which have not been published in the account of De Vries. I expected to have the data in question this autumn but the European disturbances have necessarily upset my plans and it may be very many months before I can take up the matter.

However, I will briefly say that De Vries's identification of the sheets under consideration are to me not convincing chiefly for the following reasons. His account gives no description of the pubescence of the sepals, stems, or capsules when present. Yet pubescence is a character of great importance in the description of many species of *Œnothera*. To illustrate the point, all races of *O. grandiflora* Solander that I know have sepals and capsules almost glabrous or very sparsely pilose and puberulent. *Lamarckiana* on the contrary presents sepals and capsules with a very heavy puberulent and pilose pubescence. Should any of the specimens at Paris which De Vries has identified with the *Lamarckiana* of his cultures present sepals or capsules lacking the heavy pubescence of this plant the fact to me would be very strong evidence that his identification was incorrect.

There are two sheets under consideration as standing for the type of *Œnothera Lamarckiana* Seringe. De Vries regards one as unequivocally representing the type specimen. I have for various reasons placed the greater emphasis upon the other. Both specimens as shown in photographs appear to have essentially the same features as to their general morphology. Miss

Eastwood and M. Gagnepain who compared the two specimens reported to me that they were very similar. Both were undoubtedly known to Lamarck since the two sheets bear his handwriting, and it is quite possible that Lamarck based his description on both specimens.

The general morphology of these specimens presents several features that are not those of the *Lamarckiana* of De Vries's cultures. Chief among these are (1) the approximate branches, (2) the foliage of narrower and more distinctly petioled leaves, (3) the inflorescence more open and with narrower bracts, (4) the buds more slender and tapering, and apparently with more attenuated sepal tips, (5) the long delicate hypanthium. In these features the specimens are closer to *O. grandiflora* than to *Lamarckiana*. Such morphological characters, it is true, might vary somewhat under different conditions of growth and with the time of collection whether early or late in the season. The pubescence should give us the stronger evidence of relationship since pubescence would be little if at all affected by growth conditions or by season. Of the pubescence on one of these specimens I have Gagnepain's statement that it is close to that of *grandiflora*, but it is only fair to say that no *Œnothera* specialist has reported upon such a comparison as is desired.

Lamarck's description of the capsules of his plant as short and glabrous is a point of great importance. The capsules of De Vries's *Lamarckiana* are certainly not glabrous but they are short. In my contention that Lamarck's plant was a form of *O. grandiflora* Solander I was at first forced to assume that Lamarck must have described immature or partially pollinated capsules. I have, however, this summer grown œnotheras from Mississippi which have the rosettes, habit, foliage, inflorescence, and flowers of *grandiflora*, but which developed glabrous short capsules essentially of the same relative proportions as those of *Lamarckiana*. It is immaterial what is the origin or genetic history of these plants; systematically speaking they represent short-capsuled forms of *O. grandiflora*. Thus we now know of *grandiflora*-like types which even as to their capsules agree with the description of Lamarck. De Vries does not seem to be disturbed by the fact that the material of his cultures presents capsules with a heavy puberulent and pilose pubescence while Lamarck's description specifies a capsule "glabre."

In summary I must say that my opinion remains unchanged with respect to the affinities of the plant described by Lamarck,

Œnothera Lamarckiana Seringe. Whichever of the two speci-
mens considered above represents the type, or if both were con-
cerned in the description, the evidence is to me very strong that
Lamarck dealt with forms of *O. grandiflora* Solander. I can see
no proof or even reasonable evidence that the *Lamarckiana* of
De Vries's cultures agrees with either of the specimens from
Lamarck's herbarium. A final judgment, however, should not
be made until we have before us details respecting the pubescence
of the specimens known to Lamarck.

De Vries is very positive that two other sheets in the collec-
tions at Paris present specimens agreeing with his *Lamarckiana.*
The first of these (De Vries, Plate XVIII) is from the her-
barium of Abbé Pourret and shows material which seems to me
to offer very much the same difficulties to an identification with
De Vries's *Lamarckiana* as do the specimens of Lamarck. The
foliage of lanceolate leaves clearly petioled, the slender tapering
buds, the long delicate hypanthium; these are not characters
representative of the plants from the cultures of De Vries. They
are characters of *O. grandiflora* Solander and should the pubes-
cence prove to be similar to this species I should not hesitate to
place these specimens of Abbé Pourret among the forms of
grandiflora. Until we know the facts of the pubescence, further
discussion is unwise, but it does not seem to me that De Vries's
identification rests on good evidence.

The remaining sheet at Paris which De Vries (Plate XIX)
identifies with his *Lamarckiana* is a plant from the herbarium
of André Michaux. De Vries on historic grounds naturally
attaches importance to this sheet for if it could be established
as in agreement with his plants the fact would bear directly on
the problem of the origin of *O. Lamarckiana.* The flowers are
large and the buds rather stout as we find them in our cultivated
Lamarckiana, but the sepal tips are longer and the bracts much
narrower than in *Lamarckiana.* The most striking characters
of this specimen as shown in the photograph are the narrow
lanceolate leaves and the extraordinary length of their petioles.
That such a plant could be related to De Vries's *Lamarckiana*
which has ovate-lanceolate leaves, sessile or almost sessile, seems
to me well nigh impossible. Of the pubescence De Vries tells
us nothing, yet the numerous buds on the specimen should make
it easy to determine this character and it may become a crucial
point in judging the possible or impossible relationships of the
plant.

In the discussion which must develop from the conclusions of De Vries he has taken by far the more difficult position since he attempts an identification of herbarium material with a type very accurately known to us through widely cultivated living forms. My argument is presented primarily against his identifications. It is not in any degree necessary to my argument that I should assign the sheets under consideration to definite species. Whether this can be done for any of them time will tell and I must repeat that as evidence the character of the pubescence may prove of the greatest value. I am working on the hypothesis that the specimens of Lamarck and that of Abbé Pourret are forms of *O. grandiflora* Solander. As for the specimen of André Michaux, so many remarkable forms of *Œnothera* are coming into the experimental garden from the southern and western United States that I am quite unwilling to express at present even a guess as to its affinities.

De Vries has welcomed my suggestion that the source of the cultures of Carter and Company may have been not Texas, as they state, but England. This possibility seems to me to offer an important line of investigation of early British records and collections, but at present the suggestion appears to me nothing more than a working hypothesis, although well worthy of attention. Texas and the West have some wonderful large-flowered œnotheras and Carter and Company may have obtained from such sources a plant which later hybridizing with other forms produced the *Lamarckiana* of our present cultures. That there are American western species which will hybridize with European *biennis* and produce a synthetic *Lamarckiana* is I believe established by my present studies with *Œnothera franciscana* Bartlett.

In recent papers I have reported that first generation hybrids of *O. franciscana* pollinated by the Dutch *biennis* have the essential taxonomic characters of the small-flowered forms of *O. Lamarckiana*. They differ from *Lamarckiana* in relatively small plus or minus expressions of these characters. It was to be expected that large F_2 generations would give a wide range of variation or segregation of characters and that forms would appear much closer to *Lamarckiana* than the parent F_1 plants. This proved to be the case in F_2 cultures of last summer (1914) totaling about 1,600 plants. Among these I obtained a number of individuals which were so close to the large-flowered *Lamarckiana* that flowering shoots could scarcely be distinguished as to

pubescence, foliage, inflorescence, buds, flowers, and capsules. The rosettes were also *Lamarckiana*-like. Only in habit was it somewhat difficult to match the symmetry of *Lamarckiana*. That further selection in later generations is likely still to further improve on the results of this synthesis seems altogether probable. These studies will shortly be described in full.

I am well aware that a synthesis of a *Lamarckiana*-like hybrid even should it throw in successive generations a series of marked variants (mutants) will not be considered by De Vries and his disciples as casting doubt on the validity of the "mutation" of *Lamarckiana*. They will say that in this case the hybrid took its mutating habit from one or both of the parents. Since in my cross one of the parents is the Dutch *biennis* which Stomps has shown can produce *nanella, semi-gigas* and *sulfurea* mutants, it will be claimed that any behavior of my hybrids similar to mutation will be due not to the mixing of diverse germ plasms, *i. e.*, to crossing, but will be merely a further expression of mutating habits inherent in the germ plasm of at least *biennis* if not also of *franciscana*.

This phase of the discussion may rest until we know the future behavior of my hybrids and the possibilities of the Dutch *biennis* as a form capable of mutation. It is to be expected that Stomps will carry out his very important studies on a scale that will virtually exhaust the mutative possibilities of this species. Such a study on a close-pollinated species of *Œnothera* so well known as the Dutch *biennis* will give, it seems to me, the safest data that has yet been published by students of mutation among the *Œnotheras*. It becomes a matter of great interest to know the range of variants that such a type can produce. Similar studies among some of the wild American species should also be made. The open-pollinated assemblage of forms to which *Lamarckiana* belongs must always be open to suspicion of hybridization more or less remote in time or distant in relationship. Only prolonged experiment can establish an open-pollinated *Œnothera* as free from the taint of crossing.

It is, I trust, clear that one may believe very strongly that *Œnothera Lamarckiana* is not safe material on which to base experiments designed to test the mutation theory and yet remain receptive to evidence that may come from other sources.

BRADLEY MOORE DAVIS

UNIVERSITY OF PENNSYLVANIA,
   October, 1914